A TAXONOMIC REVISION OF *VAUQUELINIA* (ROSACEAE)

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ABSTRCT

Vauquelinia is a genus of small trees and shrubs endemic to Mexico and southwestern United States. Due to considerable overlap in vegetative characteristics, the 11 taxa are grouped into three species: *V. australis* of Oaxaca and Puebla; *V. californica* with four subspecies, subsp. *californica*, subsp. *pauciflora*, subsp. *sonorensis*, and subsp. *retherfordii* from Arizona and New México south to Durango, Coahuila and Baja California, and; *V. corymbosa* with 6 subspecies, subsp. *corymbosa*, subsp. *heterodon*, subsp. *angustifolia*, subsp. *karwinskyi*, subsp. *saltilloensis*, and subsp. *latifolia* from Hidalgo, Querétaro north to Nuevo León, Coahuila, and trans-Pecos Texas. Data on leaf, flower anatomy, as well as floral vascularization are also included.

INTRODUCTION

The genus *Vauquelinia* is comprised of eleven taxa of evergreen, sclerophyllous, shrubs to small trees native to the arid, and semi-arid lands of México and adjacent United States from Puebla-Oaxaca north to Baja California, Arizona, New Mexico, and trans-Pecos Texas. The genus is here treated as composed of three species, one species having four subspecies, another with six subspecies, and the third without infraspecific divisions.

The genus *Vauquelinia* was erected by Humboldt and Bonpland (1807) in their *Plantae Aequinoctiales* based on a collection from near Actopan, Hidalgo. The genus was named, at the urging of José Francisco Correa de Serra, a Portuguese botanist, for Frenchman Nicolas Louis Vauquelin (1763-1829), student and associate of Fourcroy, later distinguished chemist, physicist, and author, whose discoveries in chemistry carried over into botany. Hence the genus is to be cited as *Vauquelinia* Humboldt et Bonpland, or, following the recommendation presented in article 46E of the International Code of Botanical Nomenclature (Voss et al. 1983), *Vauquelinia* Correa ex Humboldt et Bonpland. The new genus contained one species, *V. corymbosa*, and the genus remained monotypic for 40 years. Botanical activity in the frontiers of the United States added a second

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species, *V. californica*, from mountains near the Gila, Arizona. A third species, *V. karwinskyi*, was named in 1879 by the Russian botanist Maximowicz from collections of Karwinsky west of Ciudad Victoria, Tamaulipas. Rydberg (1908) was the first to enumerate the genus in the Flora of North America, where he recognized four species, the above three taxa and a newly described *V. angustifolia* from the state of Chihuahua, México. Soon after, four more species were described: *V. potosina* from San Luis Potosí, México; *V. australis* from Puebla, México; *V. pauciflora* from northern Sonora near New Mexico; and *V. latifolia* from Tamaulipas, México.

Standley (1922) recognized six species in his *Trees and Shrubs of Mexico*, all of the above taxa with the exception of Rydberg's *V. angustifolia* and his recently described *V. potosina*, both of which he placed in synonymy. Since Standley's treatment two additional taxa have been described from the Chihuahuan Desert Region by I.M. Johnston in the 1940's: *V. retherfordii* from southwestern Coahuila, México; and *V. heterodon* from eastern Coahuila. The work presented here represents the first systematic treatment of the genus in over 60 years. We here describe two new taxa and recognize a total of eleven taxa in three species.

In the above noted taxonomic treatments, the taxa of *Vauquelinia* have been distinguished on the basis of various vegetative characteristics, namely leaf shape, size, serration, and vestiture. Indeed, as in several other woody genera of Rosaceae (e.g. *Cercocarpus*, *Holodiscus*, *Malacomeles*, *Rosa*, and *Spiraea*) as well as in *Arctostaphylos*, *Arbutus*, *Comarostaphylis*, *Ceanothus*, *Ptelea*, and *Quercus*, taxa of *Vauquelinia* are relatively uniform in their flower and inflorescence structures, forcing taxonomists to rely heavily on vegetative features. In *Vauquelinia* each population has a characteristic or typical leaf size, shape, and serration along with an often perplexing amount of leaf variation that frequently falls well outside the expected range of variation. Some of this aberrant leaf variation is genetically based and represents extremes in genetic variation in a population. For example, plants surviving in extreme arid microhabitats commonly have smaller leaf blades—i.e., representing the survivors in a process of strong natural selection on seedlings. Similar reduced blades have been encountered when plants are under heavy grazing pressures. Other plants, perhaps occurring in more favorable microhabitats, have larger or more coarsely serrate leaf blades, and this variation must be incorporated into the range of variation of the taxon. Even on one plant, the first- and last-formed leaves of a season's increment are usually smaller and sometimes will differ in shape and serration from the others on the same stem. The average leaf shape, size, and marginal toothing and other features will also vary between disjunct

populations. In many instances populations are confined to slightly more mesic canyons in arid mountains where they occur as relicts of a perhaps more widespread distribution during the Holocene. Variation in leaf vestiture is also encountered.

It is, however, misleading to state that no taxonomically useful characteristics occur in flowers and inflorescences. Both quantitative and qualitative differences do occur in flowers involving size differences in petals and sepals, and the presence or absence of such features as glands along the sepal margins. However, as flowers are not present on all specimens it is difficult to assess the variation in these characters and to use these characters for identification. Generally we find there is considerable variation in floral characteristics as well. We therefore continue to emphasize vegetative (leaf) characters in our treatment as: 1) leaves are present on all specimens and; 2) the majority of plant collections can readily be identified on this basis. To accommodate the often wide range of leaf variation we discuss and present illustrations of many of these aberrant leaf types.

It has been somewhat disconcerting to find that the broad range of leaf variation encountered in some populations of *Vauquelinia*, as in taxon *corymbosa*, includes types completely referable to other taxa, e.g., taxon *heterodon*, and likewise to find occasional *heterodon*-like as well as *angustifolia*-like leaf characteristics in populations of taxon *karwinskyi*. It is unknown whether these extreme morphotypes indicate past introgression between these now disjunct taxa or are merely representative of the great potential of genetically-based variation in these apparently outcrossing taxa. But because of this wide degree of variation inherent in these taxa it becomes difficult to recognize them as distinct species. Whether they also contain isolation mechanisms that would allow them to retain their differences should they ever become sympatric is also unknown, but the diversity encountered in the taxa indicates that they may interbreed freely with other such taxa.

Because of the overlap in morphological characteristics and the lack in true qualitative differences separating these taxa, we recognize only three species in the genus and relegate other taxa to subspecific rank. The three species recognized include: 1) *Vauquelinia australis* Standl. (with no subspecies), occurring south of the transverse volcanic belt in the states of Puebla and Oaxaca, México and characterized by mostly oblanceolate, bicolored leaves with revolute, closely serrate margins; 2) *Vauquelinia corymbosa* Humb. et Bonpl., with six subspecies occurring along the Sierra Madre Oriental axis from Hidalgo-Querétaro north to Nuevo León-Tamaulipas and spilling into the Chihuahuan Desert to trans-Pecos Texas

and eastern Chihuahua characterized by ovate to linear, mostly glabrate leaves mostly with relatively coarse marginal serrations; and 3) *Vauquelinia californica* (Torr.) Sarg., with four subspecies occurring from Arizona and New Mexico south to Baja California and along the eastern slopes of the Sierra Madre Occidental with disjunct populations in central Coahuila characterized by lanceolate to linear, glabrate to bicolored leaves with relatively fine marginal crenulations to serrulations. We feel this is the most supportable taxonomy in which the species are reasonably well defined both morphologically and geographically and the subspecies are defined on the basis of quantitative differences in leaf shape, toothing, and vestiture, as well as geographical distribution. In all but one instance the subspecies are allopatric, occurring mostly in widely disjunct population series. In areas where subspecies of *V. corymbosa* and *V. californica* apparently have been sympatric in the past, populations showing hybrid characteristics occur at present.

Fossils of leaves considered to belong to *Vauquelinia* are recorded from two fossil floras in the western United States. In the mid-Tertiary Florissant beds in Colorado (lower to mid-Oligocene—30 mybp.) MacGinitie (1953) reports two Vauquelinias: *V. liniara* MacGinitie, with linear leaves considered to be referable to *V. angustifolia* and; *V. coloradensis* (Knowlton) MacGinitie with more obovate leaves considered closest to *V. californica*. In the mid to upper Eocene Green River flora MacGinitie (1969) reports one species *V. comptonifolia* (Brown) MacGinitie that he again refers to *V. californica*.

Recent discussions have questioned the relationships of *Vauquelinia* within the Rosaceae. In traditional classification schemes the North American *Vauquelinia*, *Lindleya*, *Lyonothamnus* and the South American *Quillaja* and *Kageneckia*, as well as the Asiatic *Exochorda* have constituted the subfamily Spiraeoideae, tribe Quillajeae, characterized by woody habits, five carpels opposite the sepals, winged seeds and either capsular or follicular fruits (Maximowicz 1879). Cytological studies by Goldblatt (1976) have suggested that *Vauquelinia* ($n = 15$) and *Lindleya* ($n = 17$) should be transferred from the Spiraeoideae ($x = 9$) to the paleoamphiploid subfamily Maloideae = Pomoideae) ($x = 17$), while *Exochorda* ($n = 8$) should be transferred to the Prunoideae ($x = 8$) and *Lyonothamnus* ($n = 27$) should be retained in the Spiraeoideae. He further suggests that *Kageneckia* ($n = 17$) and *Quillaja* ($n = 14$) are primitive in the family and should constitute a separate subfamily. The work of Sterling (1966) on comparative anatomy of the carpel of the Rosaceae independently noted the similarities in ovaries of *Vauquelinia* and *Lindleya* to those of the Maloideae. *Vauquelinia* is most closely related to *Lindleya*, and the latter differs from

Vauquelinia in a large number of features, including: 1) completely united carpels that form spheroid, five-celled, woody capsules; 2) paired, epitropic (not basal) ovules; 3) usually solitary, larger, showier flowers; 4) chromosome number (see above); 5) smaller, less coriaceous leaves; and a large number of additional characteristics.

The emphasis in this treatment is largely morphological. Our descriptions are based on extensive and intensive field and herbarium observations. We present detailed descriptions of the anatomy of vegetative, floral and fruiting structures to serve as a database for comparative studies. We also discuss the question regarding relationships of *Vauquelinia* in the Rosaceae and present keys for identification and descriptions of all taxa in the genus. No attempt is made here to indicate phenetic or phylogenetic relationships between the taxa other than that inherent in our classification.

MATERIALS AND METHODS

Herbarium specimens were borrowed from A, ARIZ, ASU, CAS, ENCB, DS, F, GH, JEPS, LL, MO, MEXU, MICH, NY, POM, RSA, SD, TEX, UC. All taxa were observed in the field during various trips in the late 1970's and in connection with the Chihuahuan Desert Flora project. Anatomical studies incorporated standard paraffin techniques for production of serial sections of leaves and flowers. SEM photomicrographs were taken with a Jeol JSM T-200 at the biology department of California State University, Los Angeles,. All plant measurements were made from dried materials unless otherwise noted.

RESULTS

COMPARATIVE ANATOMICAL STUDIES: In the section that follows we present detailed, though brief, baseline descriptions of the anatomy of stems, leaves, flowers, fruits, and seeds. Pertinent comparative data between taxa of *Vauquelinia* are emphasized. We feel this information will be important in anatomical comparisons with other potentially related genera.

Growth Habits:Taxa of *Vauquelinia* range from multi-stemmed shrubs (fig. 1a) to single-trunked trees. Arboreal taxa occur in more mesic montane habitats, or where they have been free of various perturbations. In more arid regions plants commonly occur in rocky habitats, occasionally growing in crevices. Plants may die back during extreme droughts and send up new basal shoots in favorable times. Williams (1971) notes the adverse effects of fire on growth habits of plants in southern Arizona and the tendency of the plants to produce basal sucker shoots after fire damage.

Stem Structure: Young stems are covered with a dense to thin vestiture of crinkled, uniseriate, unicellular trichomes that is generally lost after the first year. The outer cortex contains collenchyma and many tannin-containing cells, and the inner bark contains large initial bundles of phloem fibers. Secondary phloem produces masses of fibers that eventually are built into the periderm. Primary vascular tissue is in a closed cylinder.

Fig. 1. Growth habit, leaves, flowers of *Vauquelinia*. a-b.—*V. californica* subsp. *californica*. a.—Typical growth habit of small tree ca 2.5 m tall with multiple basal stems. From Catalina Mountains, Pima County, Arizona. b.—Leaves are erect-ascending, slightly folded along midrib. (*Henrickson 20289*). c-d.—*V. corymbosa* subsp. *heterodon*. c.—Leaves and corymbose inflorescences. d.—Flowers. (*Henrickson 16171*) Scales in b-d = 1 cm.

Pith lignifies in time. The first phellogen develops in the outermost cortex layer immediately beneath the epidermis. Older stems have a smooth, gray to dark gray bark. In older trunks outer bark peels, becomes vertically plaited, and generally is dark gray to black in color.

Nodal Vascularization: Nodal vascularization in *Vauquelinia* is three-trace, tri-lacunar, with lateral traces separating from the vascular cylinder slightly below the medial vascular trace. The three traces join in the lower, flattened portion of the petiole above the point of eventual abscission and continue up the petiole-midrib as a single, massive, crescent-shaped trace. Small stipular traces diverge from the outer margins of the lateral trace at the petiole base. Axillary bud traces separate from the inner margins of the medial gap and join shortly above.

Leaf Anatomy: Leaf blades are coriaceous, bifacial, and range from 0.25 − 0.52 mm in thickness. New leaves are produced in the spring on shoots that terminate in an inflorescence. Older leaves persist until after the new leaves have matured, generally abscissing from mid-late summer to winter. Leaf-blades are flat or slightly folded along the midrib with margins flat or very slightly decurved (fig. 1b-c), or in *V. australis* strongly revolute. Epidermis cells on both surfaces are pentagonal to polygonal (Dilcher 1974) with straight anticlinal walls. Those over the mid to tertiary series of vascular bundles (those with bundle sheath extensions) are elongated parallel to the subtending bundle, rectangular with straight or oblique end walls. Cuticles range from (4.5 −)7 − 14 μm in thickness, are typically thicker on the upper surface, and lack cuticular relief, though the outer tangential walls may be somewhat thickened medially, forming low papillae. The lower epidermis of *V. corymbosa* subsp. *corymbosa* and subsp. *heterodon* often develops waxy surface deposits, consisting of localized masses of vertically-oriented platelets (fig. 2c − d). They were not seen in other taxa. Leaves of *V. corymbosa* subsp. *latifolia* are distinctly glaucous on both surfaces. *Vauquelinia australis* and some subsp. of *V. californica* are variously vestitured on the lower surface and around the midrib of the upper surfaces, as well as on stems, inflorescences, etc. Trichomes in all these taxa are cylindrical, tightly curled to crinkled, 6 − 7 μm in diameter with thickened walls that leave a reduced lumen to 2 μm in thickness (fig. 2b).

Stomata are restricted to the lower epidermis, are randomly oriented, and lacking over vascular bundles with bundle sheath extensions. Guard cells range from 25 to 34 μm in length, are superficial, accompanied by a thinning of cuticle that forms a weak exterior ledge, and are subtended by 6 − 9(− 10) subsidiary cells in one series (cyclocytic). In surface view subsidiary cells overlap the guard cells.

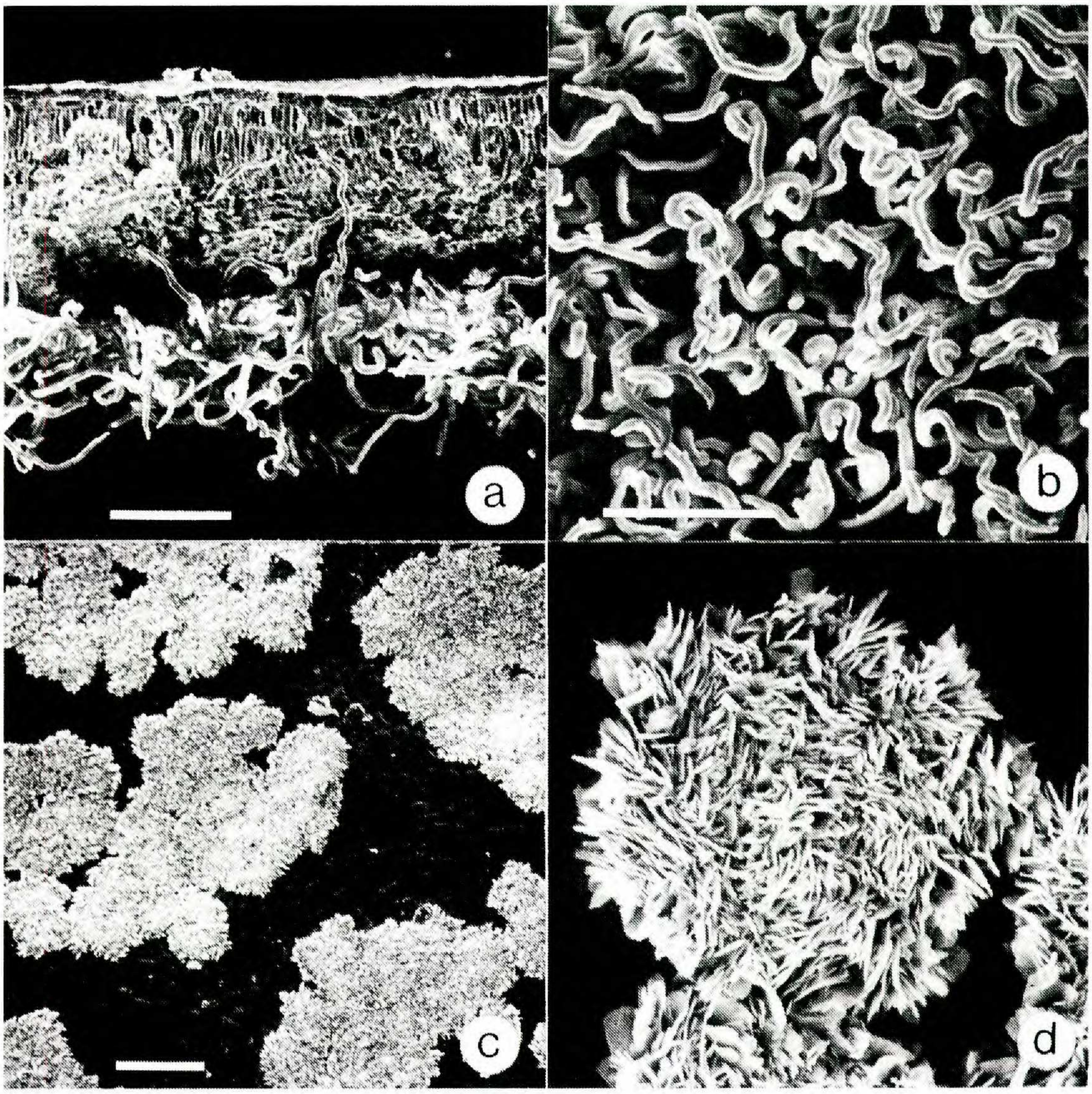


Fig. 2. Scanning electron micrographs of leaves of *Vauquelinia*. a.—*V. californica* subsp. *sonorensis*. Cross section of leaf showing dense abaxial vestiture. (*J.M. Tucker 2427*). b.—*V. californica* subsp. *retherfordii*. Abaxial leaf vestiture showing characteristic crinkled trichomes. (*Stanford et al. 87*). c-d.—*V. corymbosa* subsp. *c*. Lower leaf surface showing distinctive accumulations of vertical wax platelets. (*C. Mason 2621*). Horizontal bars in a-c = 0.1 mm, central mass in d is ca 0.1 mm in diameter.

As seen in cross sections, the upper epidermis is commonly subtended by a single (rarely double in *V. c.* subsp. *karwinskyi*) hypodermal layer usually distinguished by inclusions of saffranin-staining, tannin-like substances. In most species hypodermis is not complete but merely represents broad lateral extensions of the bundle sheath extensions (fig. 3a). A less well developed hypodermal layer may also occur next to the lower epidermis, again associated with bundle sheath extensions, but here it is interruped by substomatal chambers. Mesophyll consists of (1−)2−3(−4) tightly packed palisade layers dorsally and a relatively

dense (fig. 3a) to moderately open (fig. 3b), vertically-arranged series of cells ventrally. These ventral cells are sometimes tightly arranged in a palisade-like configuration, particularly under vascular bundles without lower bundle sheath extensions (fig. 3a), or immediately adjacent to these extensions. The midrib and secondary, tertiary, and in some taxa the 4th

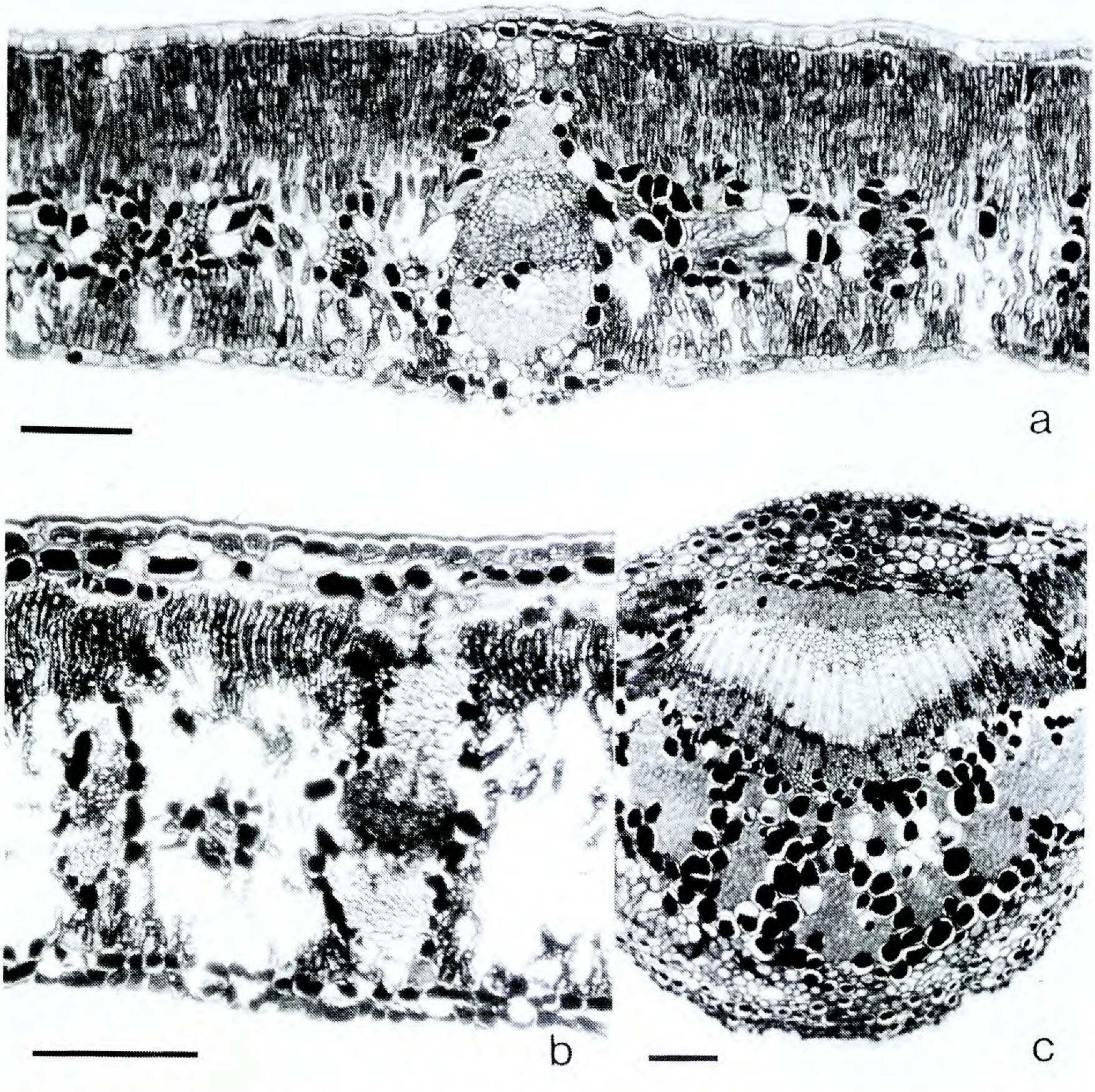


Fig. 3. Leaf structure in *Vauquelinia*. a.—*V. californica* subsp. *californica*. Cross section of leaf, showing multiple palisade layers. Largest vascular bundle has bundle sheath extension and large bundles of fibers opposite xylem and phloem. Bundle sheath extensions are absent in smaller veinlets. Note tannin-filled hypodermal and bundle-sheath cells. Leaf is ca 0.3 mm thick. (*Hess & Wilhelm 4253*). b.—*V. corymbosa* subsp. *heterodon*. Cross section of leaf showing distinct hypodermal layers and very open mesophyll. Note masses of fibers on both sides of vascular bundles. Leaf is ca 0.3 mm thick. (*Henrickson 16971*). c.—*V. corymbosa* subsp. *angustifolia*. Cross section of midrib showing extensive series of fiber bundles opposite phloem. Note dark, tannin-filled cells. Section is to ca 0.83 mm thick. (*Henrickson 15075*). Horizontal bars all = 0.1 mm.

and 5th series of vascular bundles have bundle sheath extensions continuing to both epidermises. The vascular bundles and extensions are surrounded by a single-layered bundle sheath typically distinguished by tannin-like inclusions (fig. 3a—b). The midrib, secondary, and tertiary vascular bundles all have active vascular cambia revealed by the orientation of xylem and phloem cells, and have two well developed bundles of fibers, the larger opposite the phloem and representing primary phloem fibers, the other smaller series opposite the xylem (fig. 3a—c). Between the vascular bundles and hypodermis are parenchyma cells typically packed with cuboidal, prismatic, or rather irregularly shaped or druse-like crystals.

The midrib vascular bundle (fig. 3c), as noted previously, is very large, crescent-shaped, and with an obvious functional vascular cambium. It has a series of large fiber bundles outside the phloem separated by series of large, tannin-filled cells. The similar, continuous series of fibers opposite the xylem is smaller. The tissue outside the fibers consists of parenchyma and lacunar collenchyma, some with crystals, and some with tannins (dark staining cells). In *V. californica* veinlets of the 4-5 series lack bundle sheath extensions and consist of only xylem and phloem surrounded by a single bundle sheath layer. The smallest veinlets contain only xylem. In the thickly coriaceous leaves of *V. corymbosa subsp. latifolia*, however, bundle sheath extensions occur on even the 4—5 series of vascular bundles (fig. 4a). In this instance the pattern of vascularization is reflected in fiber bundles opposite the xylem and opposite the phloem. In cleared whole leaf material, the xylem fiber series could be separated completely from the phloem fiber series.

As seen in leaf clearings (fig. 4), venation is pinnate and semicraspedodromous (Dilcher 1974). Midveins are straight and massive, and generally constitute 4—5 percent of the leaf-blade width. Secondary veins are irregularly divergent from the midvein at acute angles, often paralleling the midvein before the point of divergence (fig. 4d), either straight or upcurved distally, sometimes with the distal secondary veins of the leaf blade more acute than the mid-lower veins. Secondary veins may variably fuse and branch before the margin (not all terminate in marginal teeth) but join with superadjacent veinlets through prominent marginal fimbriae or branches. All species are distinguished by series of irregular, composite intersecondary veins originating from the midvein that are usually moderately prominent, straight near the midvein but are more zigzagged, and evidently composed of tertiary veins near the margin (fig. 4). The intersecondary veins are highly variable in development, sometimes being prominent and fusing with secondary veins, and at other times gradually

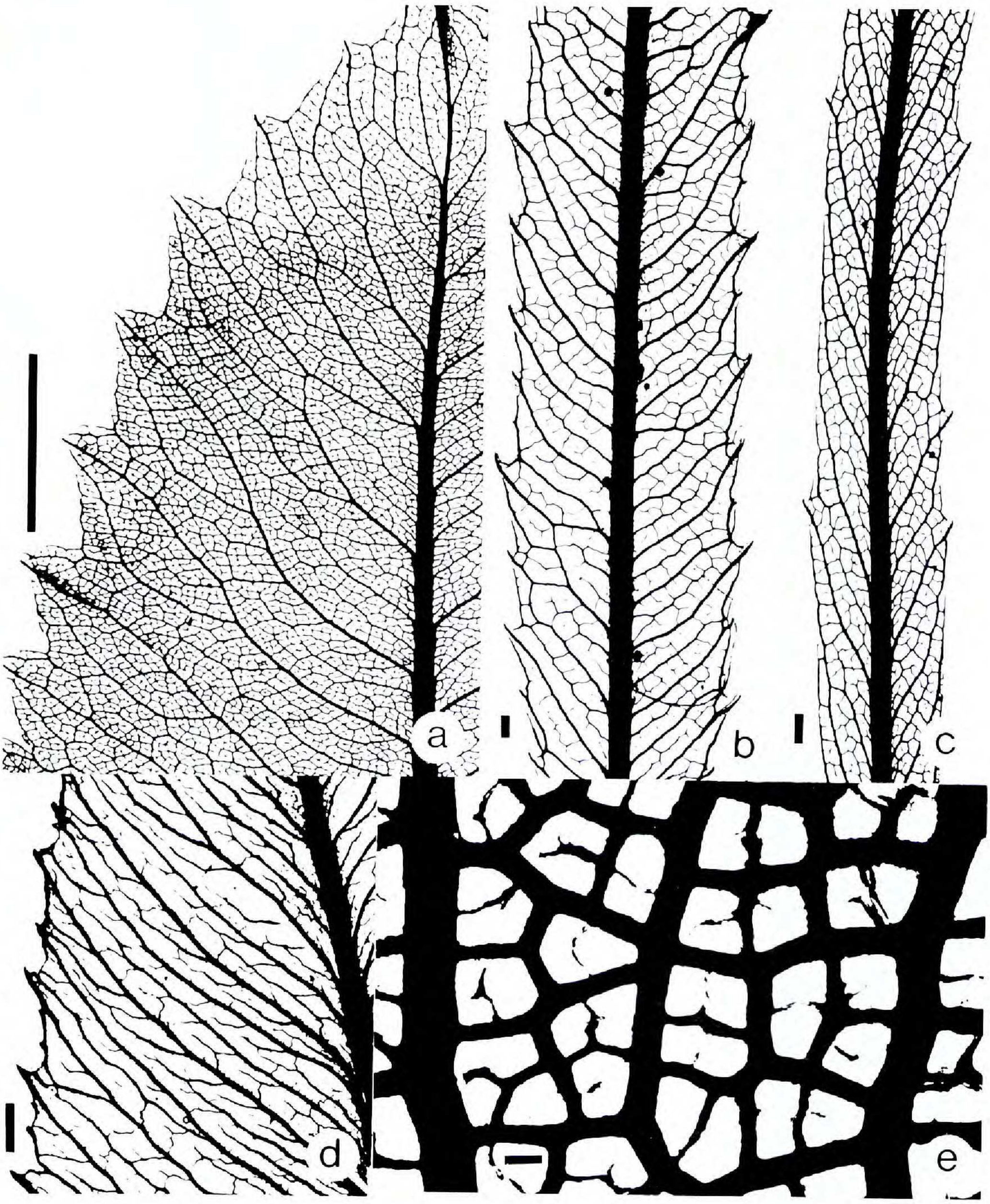


Fig. 4. Cleared leaves of *Vauquelinia* showing stained venation. a.—*V. corymbosa* subsp. *latifolia*. In this taxon the midrib to 5th series of veinlets all have bundle sheath extensions with 2 series of fibers. (*Henrickson & Hess 19235*). b.—*V. corymbosa* subsp. *heterodon*. Note intersecondary veinlets. Leaf is to ca 10.5 mm wide. (*Henrickson 16871*). c.—*V. corymbosa* subsp. *angustifolia*. Leaf is to 4.3 mm wide. (*Henrickson 15075*). d.—*V. californica* subsp. *californica*. Note differences in minor venation. (*Hess & Wilhelm 4253*). e.—*V. corymbosa* subsp. *corymbosa*. Enlargement of secondary and minor venation. Two largest vertically-oriented veins are secondary veins, the medial large vein is an intersecondary vein. Bundle sheath fiber masses extend to quaternary veins but not to 5th series. (*Hess & Wilhelm 4371*). Horizontal bars in a = 1 cm; in b-d = 0.1 mm; in e = 0.01 mm.

diminishing near the leaf-blade margins. They are least developed in collections of *V. californica* subsp. *californica* (fig. 4d). Tertiary veinlets usually arise alternately, more or less at right angles (fig. 4a–c, e) or sometimes at acute angles (fig. 4d) to the secondary veins; they are variously joined (percurrent) and forked to a 4th or 5th degree of branching with intercostal areas producing series of triangular to polygonal orthogonal reticula (fig. 4e). Areoles are small, well developed, occasionally imperfect, ranging from triangular to polygonal in outline and have simple or variously once (-twice) branched veinlets.

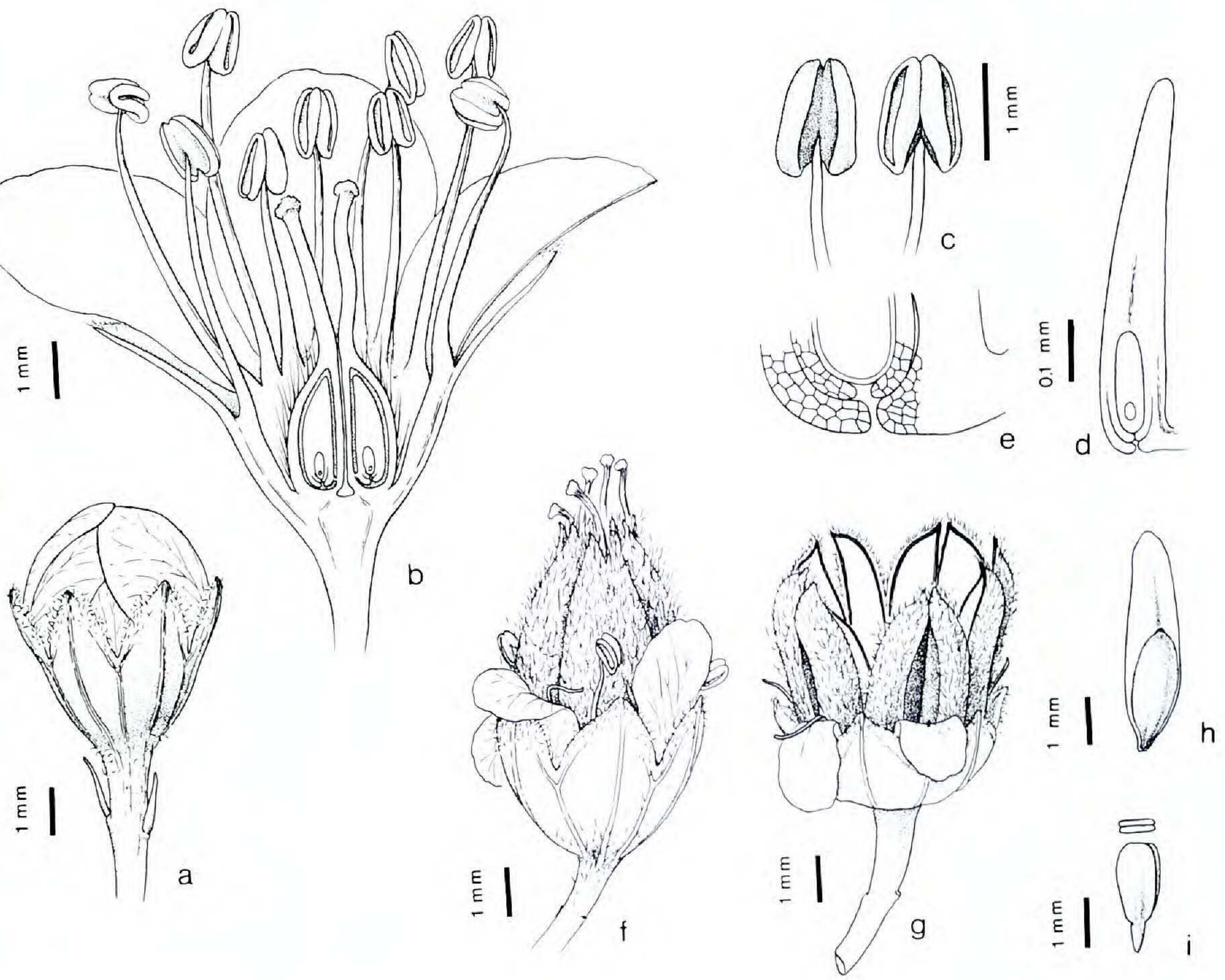
Inflorescences: Flowers are borne in compound corymbs (figs. 1c, 10a). The lowermost peduncles are subtended by reduced leaves (fig. 10a). Upper bracts and bracteoles are membranous, linear-subulate, and commonly beset with marginal glands.

Flowers: Hypanthia: Pedicels terminate in thick-walled, coriaceous hypanthia (fig. 5b). In bud stages the hypanthium and sepals may be densely vestitured, but they are generally glabrate with age. The basal outer hypanthia are commonly pentagonal, with the angles opposite the mid-sepal line. The inner hypanthium surface around the ovary is nectariferous and contains many stomata.

Sepals: The hypanthium terminates in five deltate, coriaceous sepals with narrow, membranous margins. In bud the sepals are valvate (fig. 5a), often strongly vestitured outside and along the inner margins. This vestiture usually diminishes in extent by anthesis, but a dense marginal tomentum commonly persists. Representative sepal vascularization is shown in fig. 6m. The membranous sepal margins commonly contain series of marginal glands in taxa of *V. californica*. Sepals persist as erect structures around the fruit (fig. 5f–g).

Petals: Petals are white, imbricate in bud but spreading at maturity. Each petal receives a single trace from the hypanthium, but this soon divides and anastomoses above (fig. 6n). Most petals are somewhat oblong to oblong-ovate, oblong-obovate, entire, rounded or sometimes retuse apically and have short, broad claws at their bases. In taxa characterized with strong vestiture they are often densely covered with trichomes where exposed in bud, but the vestiture falls away prior to anthesis. Occasionally some hairs persist at the petal tip at anthesis. In some taxa the petals are caducous, in others they recurve and persist around the fruit (fig. 5f).

Fig. 5. Flowers, fruit and seeds of *Vanquelinia*. a-e.—*V. corymbosa* subsp. *heterodon*. a.—Bud showing two bracteoles, sepals with conspicuous external venation and marginal vestiture, and imbricated petals. b.—Diagrammatic cross section of open flower showing central space between ovaries, styles, position of ovules, hirsute vestiture on exterior of ovaries, stamens, and perianth. c.—Stamens showing anthers in abaxial (left) and adaxial (right) view. (all *Henrickson 16076*). d-e.—Embryo structure.



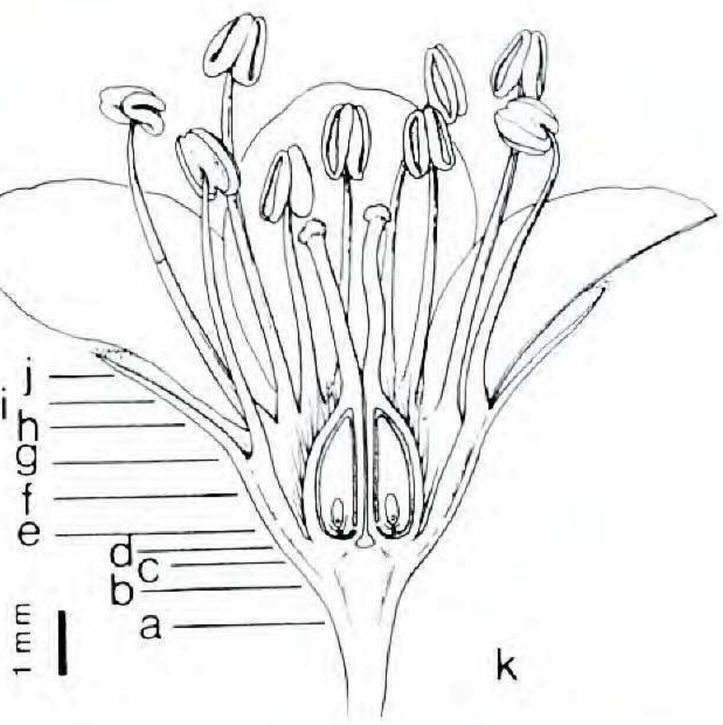
d.—Embryo ca 1.25 mm long with two integuments, tissue above embryo sac stains darkly. Note vascular trace in funiculus. e.—Detail of integuments and micropyle. Embryo sac measures 8 um in width. (*Henrickson 16971*). f-g. Mature fruits of *V. californica* subsp. *sonorensis*. f.—Closed fruit showing sepals, persistent petals, and styles. g.—Open fruit showing persistent sepals, and carpels that separate completely along ventral suture and partway down dorsal suture. Outer walls are hirsute; inner pericarp surfaces are smooth and dry. (*Henrickson 20283*) h-i.—*Vauquelinia californica* subsp. *californica*. h. Seed showing basal embryo and terminal wing. i.—Embryo showing structure and cross section of cotyledons. Magnifications as indicated.

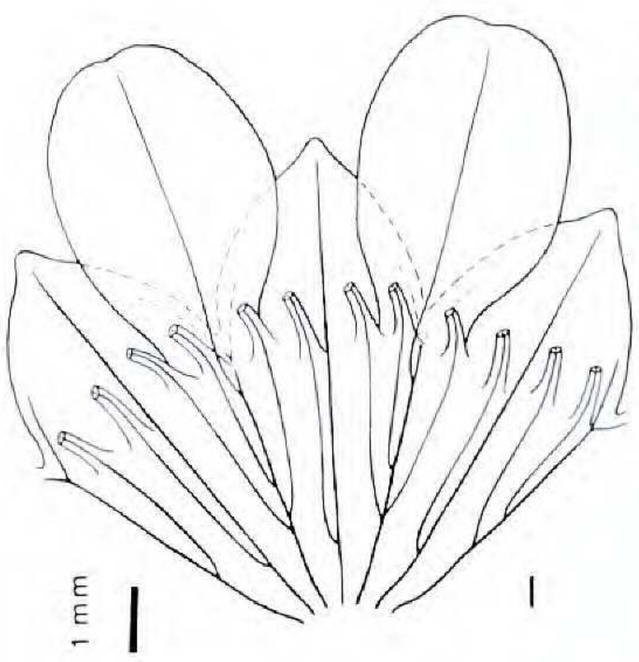
ANDROECIA: Most flowers have 18 – 20 stamens, with 20 the expected number (see floral vascularization section). The stamen series opposite the sepals are separated from the hypanthium slightly before the others, while the three stamens opposite each petal are briefly and marginally adnate to the basal inner petal margin, and their filaments separate more or less simultaneously. Except for the first series, stamens are not produced in distinct whorls. Filaments are subulate, glabrous, white, often abruptly expanded at the base where they may be briefly connate (fig 5b). Anthers are bithecate, tetrasporangiate, glabrous, yellowish-gold, and introrsely dehiscent (fig. 5c). They have glandular tapeta, and the anther-sac walls are three cells thick. Pollen is tricolporate, and prolate. Exine is thin, and the grains commonly collapse when cleared. Sexine sculpturing is tectate, very finely reticulate with 9 – 12 reticula per 5 μm that form into distinct striate patterns that continue across the polar regions (fig. 7d). Cleared pollen measured 23.5 (range 19 – 29) μm in equatorial diameter, 22 (range 17-26) μm in polar diameter.

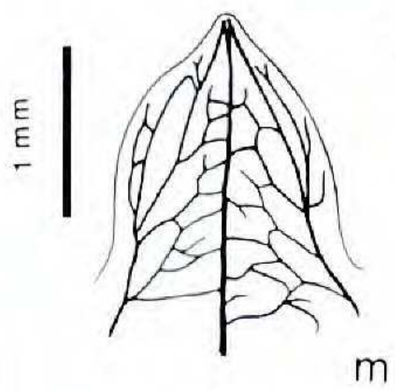
GYNOECIA: The ovary consists of five carpels, is sessile on the receptacle (fig. 5b), and is only slightly adnate at its lower margins to the hypanthium. Each carpel contains two erect apotropous ovules in a single locule (fig. 6g, Sterling 1966). Ovules are elongate, with the terminal portion eventually developing into a seed wing (fig. 5d). Two integuments line the basal micropyle (fig. 5e). The embryo sac forms near the base of the ovary, contained in a crassinucleate nucellus that is surrounded by a single layer of tannin-containing cells. At the ovary base carpels are adnate all along their margins, and their inner (ventral) sutures are usually closed (fig. 7a – b). Above the ovary base the outermost portions of the carpels separate. Each carpel receives three vascular traces, a distinct dorsal trace and two ventral traces that divide into wing and ovule traces at the base of the ovary (fig. 6e – f, Sterling 1966). Both wing and dorsal traces continue into the style (fig. 6j). In fruit additional vascular tissue becomes apparent in the ovary wall. The outer portion of the ovary is strigose, covered with erect, stiff, lignified trichomes. Styles are short, erect, thickened distally, and terminate in truncate to oblique, rounded styles (fig. 5b). Dried styles often persist on the fruit (fig. 6f).

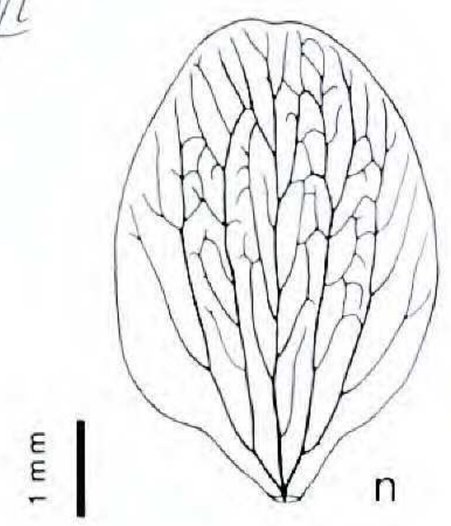
Floral Vascularization: The pattern of flower vascularization was determined from cleared and paraffin-sectioned preserved floral materials of three taxa—*V. corymbosa* subsp. *heterodon*, *V. c. subsp. angustifolia* and *V. californicia* subsp. *retherfordii*. All are basically similar in vascularization pattern, though some minor variations were noted (fig. 6).

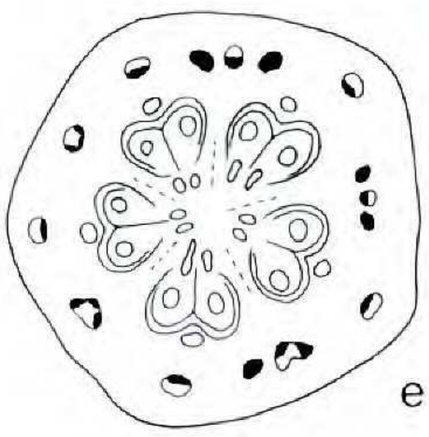
Vascular tissue in the pedicels organizes into a series of 10 peripheral traces that extend centrifugally into the base of the hypanthium or floral

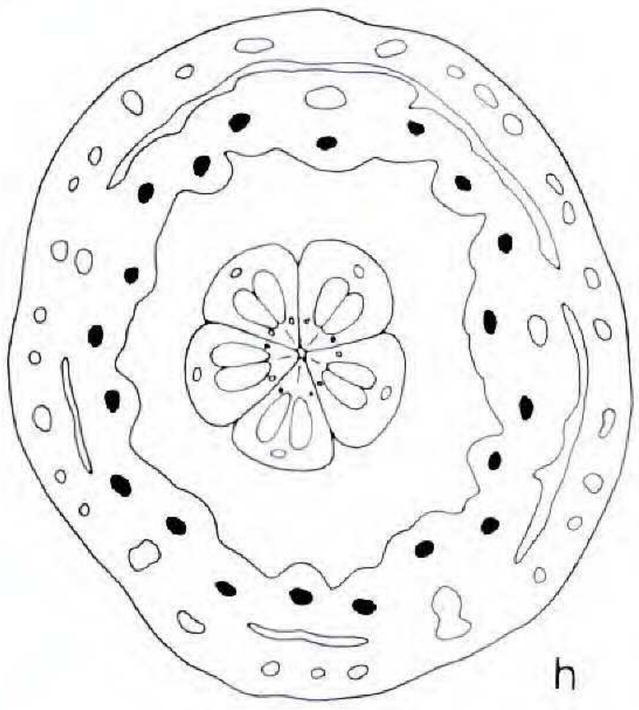


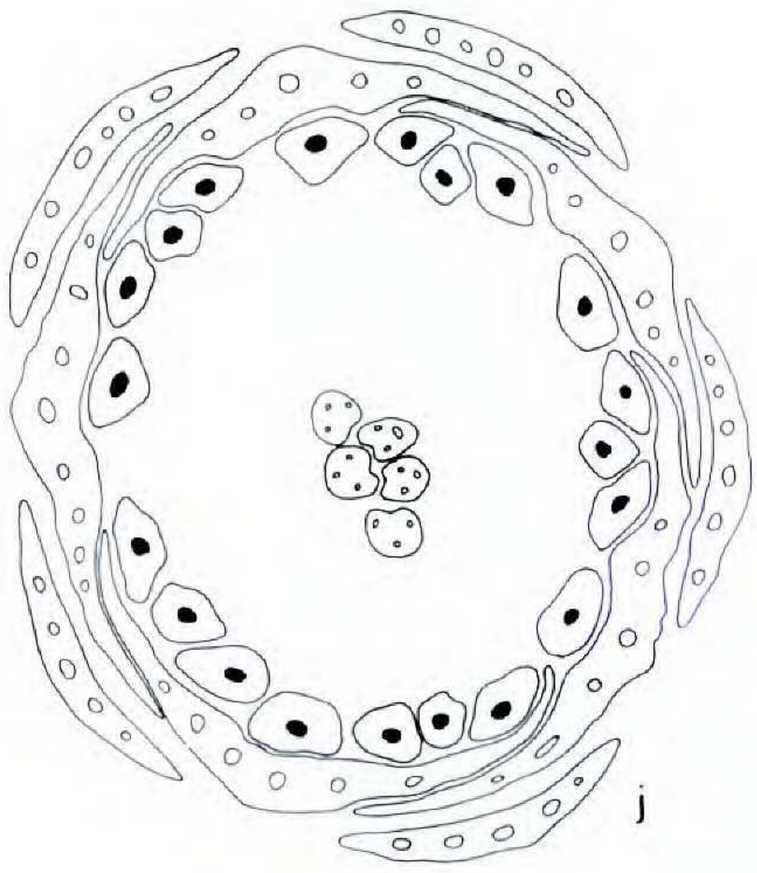


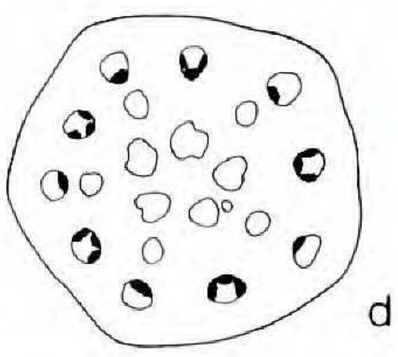


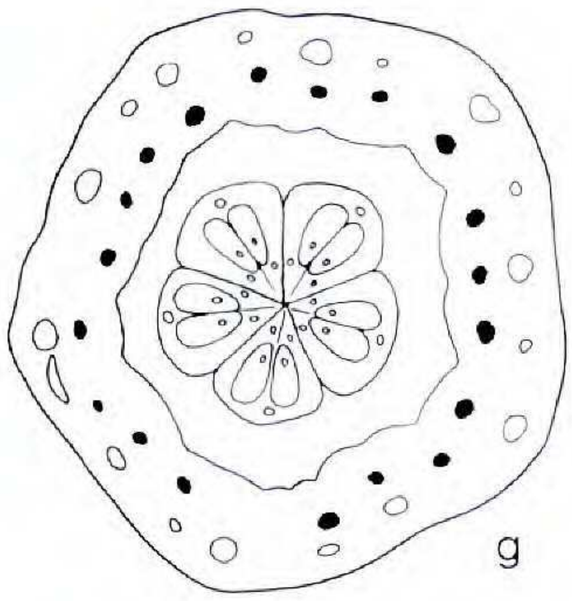


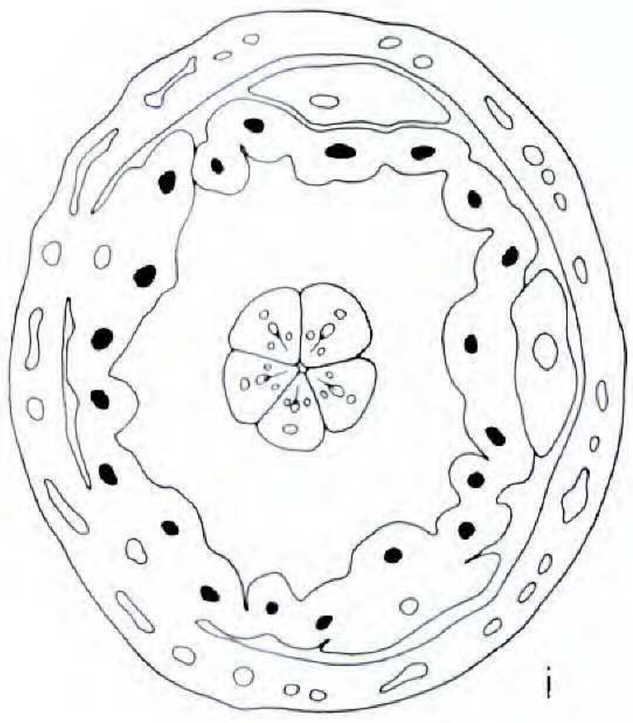


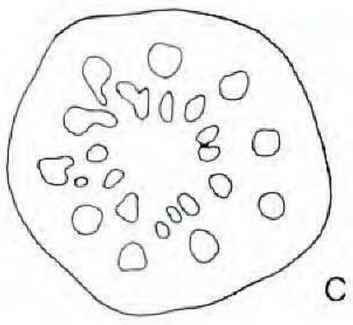


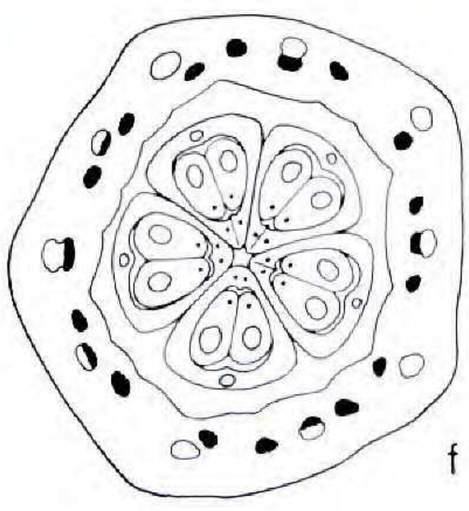


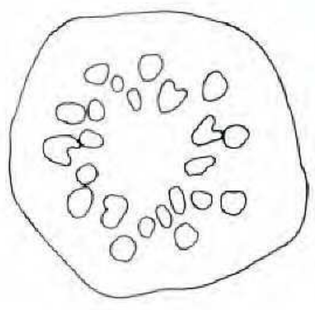












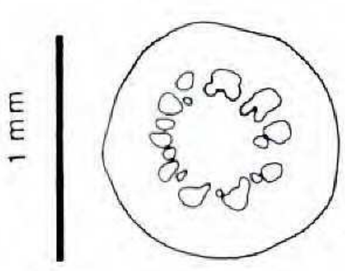


Fig. 6. Vascularization of flowers of *Vauquelinia corymbosa* subsp. *heterodon*. a-j.—Diagrams of vascular system as seen in serial cross sections at levels indicated in fig. k. Stamen traces are indicated by black circles in d-j. Note that mid-sepal traces each give rise to single stamen traces; alternate traces give rise to 2 stamen traces and 1 petal trace before dividing to become marginal sepal traces of 2 adjacent sepals. Note ovary structure. l.—Diagram showing orientation of vascular traces in cleared, flattened hypanthium. Note divergence of stamen, petal traces. m.—Vascular system of sepal as seen from cleared material. Sepals receive 3 traces, one medial, and two marginal. n.—Vascular system of petal as seen from cleared material. Petals receive single traces that branch basally (all from *Henrickson 16076*). Magnifications as indicated, scale in a holds for a-j.

cup (fig. 6c – d). The remaining interior traces organize into five dorsal ovary traces opposite the mid-sepal traces, with the remainder eventually organizing into 10 ventral traces in the center of the receptacle (fig. 6c – d). The peripheral hypanthial traces consist of five mid-sepal traces located in the angles of the pentagonal hypanthium and five marginal sepal-petal traces that in the lower receptacle each have two interior, smaller, marginal traces that eventually fuse completely with these marginal sepal traces. At this level the ovary base is visible as five carpels located opposite the mid-sepal traces each capped with a dorsal trace (fig. 6e). The ovaries are obdeltate with obcordate locules as seen in cross section (fig. 6e) and, at their very base, are completely connate laterally. Slightly above the base the ovaries are separate, and their lateral borders are marked by their contiguous epidermal layers that form distinct double rows of cells (fig. 7b). Similar double rows of cells also line ventral sutures. None of the material examined here showed carpels open along the ventral sutures as reported by Sterling (1966). At a higher level the 5 ovaries are fused along the ventral sutures (fig. 6g – h) and along the inner margins of the carpel sutures; the carpels are usually free along the peripheral portion of the intercarpel suture. This fusion pattern is also evident on the mature fruit (fig. 7c).

Each carpel has a single locule and 2 basal, winged ovules that receive their ovule bundles at the very base of the ovary where the ovule bundles separate from the ventral traces (fig. 5d, 6e). The ventral traces then continue into the ventral portion of the ovary wall as wing bundles. The wing and dorsal traces extend to the top of the ovary and enter into the style (fig. 6h – j).

In the mid to lower hypanthium stamen traces emerge from the 10 peripheral hypanthial traces; first, one each from mid-sepal trace, and at a slightly higher level, a series of three traces develop from each marginal-sepal-petal trace with the two marginal traces separating below the level of the medial stamen traces (fig. 6d – i, l). Each flower then tends to have 20 stamens, occasionally fewer. At the rim of the hypanthium stamens opposite the mid-sepal trace separate first—forming what could be considered the first or innermost series of stamens (fig. 6i), but this is scarcely evident. The other stamens, all derived from the marginal sepal-petal trace, separate from the hypanthium *with* the petals and are briefly adnate to the lower, inner margin of the petals (fig. 6h – i). It is not until after the petals have begun to diverge that the solitary petal traces separate from the marginal sepal traces, entering directly into the base of the petals (fig. 6i) and soon branch into 3 to 5 traces at the petal bases (fig. 6n). Above this point marginal sepal traces give rise to series of horizontal traces in the

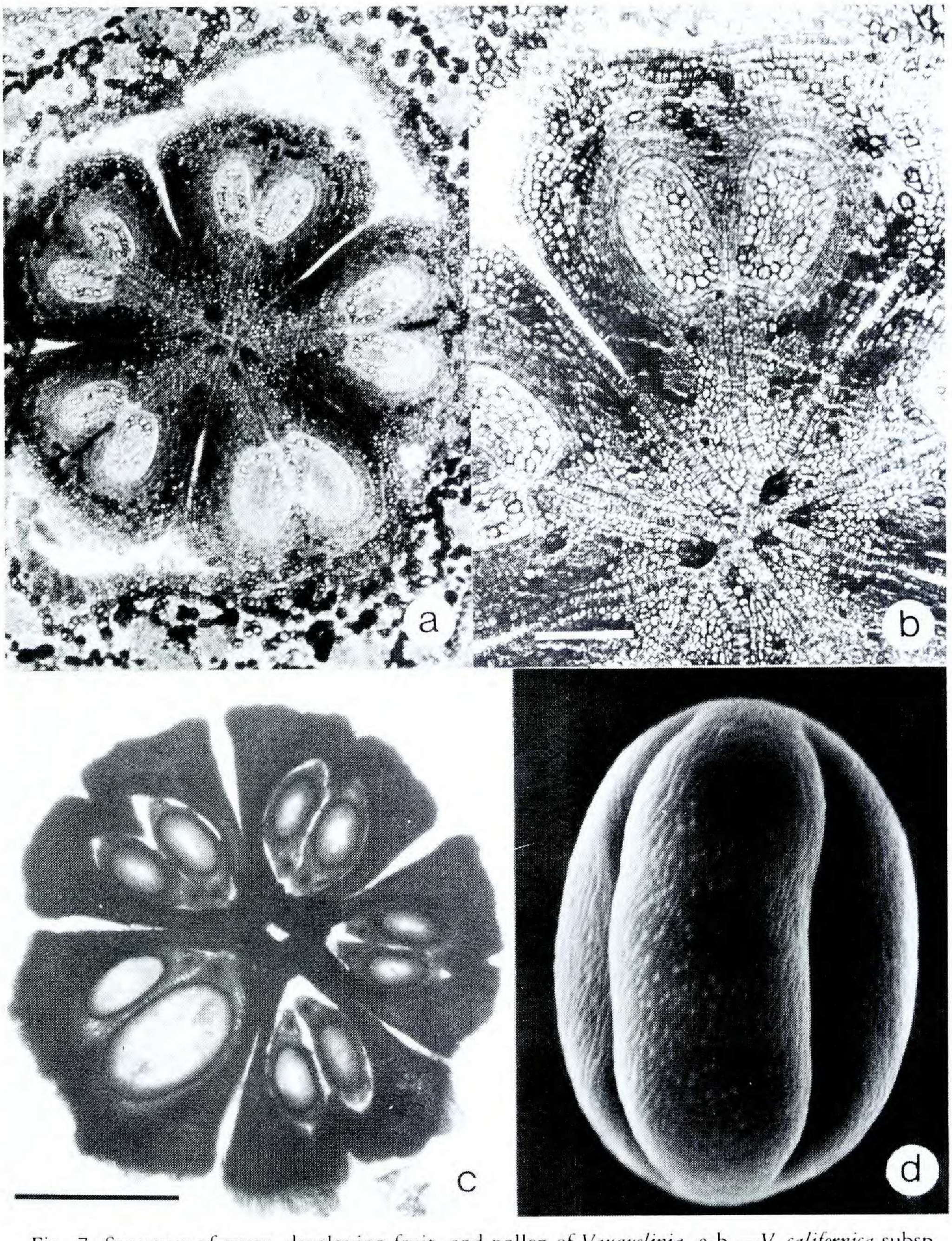


Fig. 7. Structure of ovary, developing fruit, and pollen of *Vauquelinia*. a-b.—*V. californica* subsp. *retherfordii*. a.—Cross section of ovary in young flower. Note carpels are connate centrally but separate along the outer margins. Each carpel has one locule, two ovules. Ovary is ca 0.88 mm in diameter. b.—Expanded view of single carpel showing ovules and two layers of cells forming border between carpels and along ventral suture. Carpel is ca 0.5 mm long. (*Henrickson 15874*). c.—*V. corymbosa* subsp. *corymbosa*. Hand-cut cross section of developing fruit showing 2 ovules per carpel with embryo sacs. Note carpels are connate centrally, separate marginally. (*Hess & Wilhelm 4376*). d.—*V. californica* subsp. *pauciflora*. Dry, non-acetolyzed pollen showing fine striate, finely reticulate sculpturing. (*W. W. Jones 54*). Pollen is ca 16 μm long. Horizontal bars in a-b = 0.1 mm long, in c = 1 mm, in c = 10 μm.

lower sepals and eventually branch, with one branch going to each adjacent sepal (fig. 6l – m).

Sterling (1966) noted that the configuration of the ovary, the fusion along the inner margins, and the paired basal ovules etc., was reminiscent of that found in some Maloideae. But this similarity appears only at the very base of the ovary where carpels are completely fused. Above this point each carpel has a distinct epidermal layer, and although adjacent carpels are contiguous and connivent to one another, they are not fused. Instead there is a distinct double row of epidermal cells, the same as found bordering the ventral suture in both Maloideae and *Vauquelinia*. Sterling (1964) notes that primitive Maloideae have five vascular bundles to each carpel, one dorsal, two wing bundles to the ovary wall, and two separate ovule traces that develop from a central receptacular plexus. With specialization the wing and ovule bundles develop from the basal ventral bundles. The latter situation occurs in *Vauquelinia*. Some Maloideae (*Pyracantha*) have completely separate carpels that are adnate to the hypanthium only at the very base.

Fruits: The ovary matures into a dry, ovoid, woody, capsular fruit (fig. 5f). Each carpel is connate to adjacent carpels near the center but free in the peripheral half (fig. 5f, 7c) and the developing fruit is thus marked with five vertical grooves marking the spaces between the carpels. As the fruit dries and dehisces, the carpels open all along the inner (ventral) suture, across the stylar region, and about half way down along the dorsal trace (fig. 5g). As they dehisce each carpel separates from adjacent carpels. The outer surface of the carpel is strigose, covered with lignified, stiff, erect, unicellular hairs.

Seeds: The two seeds produced in each carpel have basal dicotyledonous embryos, and no endosperm. The seed coat forms a terminal wing whose size and shape conforms to the shape of the locule. At maturity the wings are dry, glabrous, and brownish (fig. 5h).

Embryos: Embryos consist of a basal, terete radicle and two oblong, terminally rounded cotyledons (fig. 5i).

TAXONOMIC TREATMENT

VAUQUELINIA Correa ex Humboldt & Bonpland. Pl. Aequin. 1(6):140. 1807. TYPE: *Vauquelinia corymbosa* Humboldt & Bonpland.

Evergreen, multi-stemmed shrubs to small trees; young stems terete, slender, alternately branched, yellow-green to reddish- or chestnut-brown, tomentulose to villous-canescent with short, tightly crinkled white hairs, tardily to soon glabrate; bark gray to gray-black, smooth or variously fissured, or vertically plaited with age. Leaves alternate to rarely

subopposite-opposite, erect-ascending to spreading, usually variable in size with second and third leaves of a season's increment larger and with different toothing than first- and last-formed leaves; leaf-blades dorsiventral in structure, strongly to slightly coriaceous, usually corneous along margins, plain, or slightly folded along midrib, with margins revolute to variously crisped, linear, lanceolate, oblong-lanceolate, oblong-elliptic, oblanceolate to broadly ovate, acute to rounded, usually mucronate or retuse by terminal dieback at tip, narrowly to broadly, often obliquely cuneate, rounded to subcordate, with margins extending down petiole at base, at margins variously crenulate to serrate, often partially double serrate-crenulate; teeth low, rounded, to ascending-divergent, acute-acuminate, terminating in a caducous gland on inner tip margin, similar caducuous glands often borne in axils of teeth and along margin between teeth and continuing down petiole wings, gland bases persistent, usually darkened; lamina initially tomentulose with tightly crinkled hairs throughout, soon to tardily glabrate, sometimes persistently puberulent along the basal midvein, green, lustrous or dull with midvein impressed above, usually more persistently puberulent-tomentulose, more yellow-green, with venation conspicuous and midvein conspicuously raised beneath, both major and minor veins with bundle sheath extensions; petioles short to elongate, canaliculate, narrowly winged, yellow-green or reddish, puberulent-tomentulose to glabrous; stipules subulate to narrowly deltate, usually dull red-brown, initially tomentulose, glabrescent, glandular-margined, tardily caducous. Flowers borne in terminal, puberulent to tomentulose-villous compound corymbs, these often aggregated at branch tips, with lower branches developing from axils of reduced leaves, upper branches with reduced, linear-subulate, gland-margined, mostly caducous bracts-bracteoles; pedicels bibracteolate; hypanthia obconic to hemispheric, coriaceous, often distinctly veined, initially tomentulose, variously glabrate outside, nectariferous, usually glabrous above a sericeous base, persistent; sepals 5, valvate in bud, green, broadly ovate, more deltate in fruit, erect-spreading, coriaceous, strongly mucronate at tip; margins thin, rounded, often with scattered caducous glands, initially tomentulose-villous, variously glabrate to villous-tomentulose outside, usually persistently villous at least along margins and at tip inside; petals 5, inserted at mouth of hypanthia alternate to sepals, imbricate in bud, white, thickish, oblong-ovate, oblong-obovate, rounded to emarginate at tip, cuneate to rounded, sessile or broadly clawed at base, entire, spreading to reflexed, caducous or reflexed and persistent, tomentulose where exposed in bud, glabrate or floccose at tip; stamens 18 – 20, borne in more or less 1 series on the upper hypanthium; filaments subulate,

connate basally, glabrous, unequal in length and forming generally into 4 size classes with longer filaments slightly broader at base, inflexed in bud, reflexed-spreading in flower; anthers ovoid, bithecal, introrse, longicidal, subversatile with filament attached abaxially, exserted; carpels 5, opposite sepals, basally connate, and borne on a thickened hypanthium-receptacle but free from lateral hypanthium, densely sericeous; ovules 2 per carpel, attached at inside locule base, ascending, anatropous, bitegmic, prolonged apically into a thin, membranous wing; styles 5, erect, glabrous, dilated distally, broadly truncated and stigmatic at tip, yellow, turning dull brown and persisting on fruit. Capsules dark brown, woody, broadly ovoid, sericeous, surrounded by the persisting hypanthium; carpels 5, separating from one another to the base and each dehiscing ventrally to base but dorsally only in the distal half; seeds 2 per locule, compressed, ascending; embryo cotyledons flat, ovate; radicle straight, basal; testa tan to yellow, expanding distally to form a membranous oblong wing longer than the embryo, in outline conforming to locule space; endosperm absent (figs. 8 – 19).

With three species, and ten subspecies, from southern Arizona, southwestern New Mexico, west Texas south to central Baja California, Durango, Tamaulipas, San Luis Potosí, Hidalgo, Querétaro, Puebla, and Oaxaca, México (figs. 9 – 13).

KEY TO SPECIES

A. Leaf blades mostly oblanceolate, oblong-oblanceolate, broadest in the distal half with margins usually distinctly revolute to inrolled, tomentulose beneath at maturity; Puebla and Oaxaca. . . . . 1. *V. australis*

AA. Leaf-blades mostly linear to lanceolate, oblong-lanceolate, ovate or elliptical, broadest in the proximal half or middle with margins flat, crisped or slightly revolute but not inrolled, glabrous to canescent, rarely persistently tomentulose beneath; of northern distribution.

B. Leaf margins crenulate with mostly 2 – 7(– 10) low, rounded teeth per 1 cm; sepal margins without small, sessile glands; plants of northern Baja California, Arizona, to Durango, central Coahuila. . . . . 2. *V. californica*

BB. Leaf margins serrate, serrulate to doubly serrulate, with mostly 1 – 2(– 4) acute to acuminate teeth per 1 cm, when doubly serrate, secondary teeth usually low and rounded; sepal margins mostly with small, sessile, caducous glands; plants of Hidalgo, Querétaro north to San Luis Potosí, Tamaulipas, Nuevo León, eastern Coahuila. . 3. *V. corymbosa*

1. VAUQUELINIA AUSTRALIS Standl. Proc. Biol. Soc. Wash. 31:132. 1918.
TYPE: MÉXICO. PUEBLA: Cerro de Paxtle, vicinity of San Luis Tultitlanapa, Apr 1908, *C.A. Purpus 2729a* (HOLOTYPE: US!; ISOTYPES: F! GH! MO! NY! UC!).

Ovoid, multi-stemmed shrubs to small trees 2 – 8(– 10) m tall; young stems closely, densely, rarely sparsely arachnoid-villous to tomentulose

with slender, tightly crinkled, matted hairs 0.1 − 0.2 mm long, tardily glabrate to glabrate; older stems with smooth gray or gray-brown bark; basal trunks to 2 − 3(− 6) dm in diameter with dark brown, tight, irregularly plaited bark. Leaves ascending; leaf-blades oblanceolate, oblong-oblanceolate, oblong-elliptical, oblong, occasionally narrowly elliptical, usually broadest in distal half, (2 −)3 − 9(− 12.5) cm long, (6 −)10 − 24(− 32) mm wide, [length-width ratio (3 −)3.5 − 5], coriaceous, 0.2 − 0.3 mm thick, obtuse, rounded to acute, mucronate, rarely retuse at tip, narrowly to broadly, often obliquely cuneate with margins continuing down petioles at base, at margins revolute to distinctly inrolled, rarely plain and unevenly crisped, serrulate, serrate or partially doubly serrate with serrations ascending, rarely divergent, blunt or acute, corneous, 0.2 − 1.0(− 2.0) mm long, mostly 3 − 7 per 1 cm, usually tipped with caducous glands 0.1 − 0.2 mm long, sometimes with glands between major serrations; lamina usually initially arachnoid-villous to tomentulose on both surfaces, becoming glabrate, smooth, lustrous, dark green except where more persistently villous to tomentulose along impressed midvein above, more persistently gray-white tomentulose with a close covering of gray-white crinkled hairs except along raised yellow or reddish midvein, sometimes vestiture persisting only along minor venation, occasionally almost glabrate beneath; petioles (4.5 −)7 − 11(− 18) mm long, [(0.2 −)0.12 − 0.09(− 0.07) times as long as leaf blade], yellowish to reddish, adaxially canaliculate, narrowly winged by decurrent leaf margins, mostly with 4 − 7(− 12) pair of caducous glands bordering wings, moderately to sparsely tomentulose adaxially; stipules narrowly deltate, 1 − 2(− 3) mm long, caducous, villous-tomentulose, sometimes glabrate with caducous glands along margins. Compound corymbs 2.5 − 4.5 cm long, 4.5 − 7.5 cm wide, often aggregated at stem tips; lower peduncles 8 − 15(− 20) mm long; pedicels-peduncles sparsely puberulent, villous to tomentulose or tardily glabrate; upper bracts-bracteoles linear to oblong-lanceolate, 1 − 3(− 5) mm long, tomentulose-villous, with glands along margins; hypanthia hemispheric, 1.5 − 2.1 mm long, 2.5 − 3 mm wide, to 5 mm wide in fruit, loosely tomentulose, partially glabrate, greenish outside, sparsely sericeous inside; sepals broadly ovate, 1.3 − 2.5 mm long, to 1.5 − 2.1 mm wide, obtuse, strongly mucronate at tip, at margins thin with 1 − 3(− 4) pair of caducous glands, partially glabrous outside, densely tomentulose particularly along lower margins inside; petals broadly elliptic, obovate to orbicular, (3.2 −)3.4 − 5.2 mm long, (2 −)3.2 − 3.9 mm wide, rounded, rarely emarginate at tip, usually broadly clawed for 0.2 − 0.5 mm or sessile at base, initially villous-tomentulose where exposed in bud but usually

glabrate by anthesis, mostly caducous; filaments 2.6−4.5 mm long; anthers 0.7−0.9 mm long, to 1.3 mm long wet; styles 1−1.4(−2) mm long. Capsules 5.5−6.5 mm long, 4−5 mm wide, sericeous; seeds 4.5−5.5 mm long, 1−1.5 mm wide; mature embryos 2.0−2.5 mm long, 1−1.3 mm wide (figs. 8, 13).

Vauquelinia australis is perhaps the most easily recognized species of the genus, characterized by its oblanceolate, oblong-oblanceolate to oblong, oblong-elliptical, short-petiolate leaves mostly with revolute or distinctly inrolled, closely serrate-serrulate margins (fig. 8). In its typical phase, leaves are persistently, closely, gray-white tomentulose or tomentose along the reticulate minor veins beneath and lustrous, dark green above. Sepal margins bear minute glands, as in most taxa within *V. corymbosa*. However, in its persistent leaf vestiture, short petioles, small teeth and involute margins it appears more similar to *V. californica* than to *V. corymbosa*.

Populations of *V. australis* from near Tehuacán and San Juan Ixcaquixtla, Puebla are distinctive in their tendency to have smaller, more glabrate or nearly glabrous leaves with flatter, non-revolute, often sharply serrate or doubly serrate, more or less crisped margins (fig. 8d−f). Field observations by Hess from the populations near Tehuacán, indicate that these plants occur along a limestone ridge between San Lorenzo and Tehuacán and that the plants appear stunted and heavily grazed. More remote, ungrazed plants had larger, more typically vestitured, undulate or slightly revolute leaf margins characteristic of the species (fig. 8d). Label data of the collection near San Juan Ixcaquixtla also noted heavy grazing pressures. These distinctive specimens could represent heavily grazed plants bearing a juvenile leaf type. Other aspects, however, indicate that the differences exhibited are genetically based. The populations warrant additional study.

Vauquelinia australis is separated from other species of *Vauquelinia* by the trans-volcanic ranges. The importance of the Tertiary-Pleistocene trans-volcanic belt on distribution of plants in México is reviewed by Axelrod (1979).

Vauquelinia australis is known only from three populations in the state of Puebla and three from the state of Oaxaca (fig. 13), where it is locally common on limestone hillsides and canyons from 1670 to 2350 m, primarily in thorn-scrubland or chaparral with species of *Tecoma*, *Karwinskia*, *Ptelea*, *Opuntia*, *Rhus*, *Comarostaphylis*, *Juniperus*, *Lycium*, and *Berberis*. Flowering occurs from April to May.

Representative collections: MÉXICO.

2. VAUQUELINIA CALIFORNICA (Torr.) Sarg.

Rounded to ovoid, obovoid, multi- to single-stemmed shrubs to trees

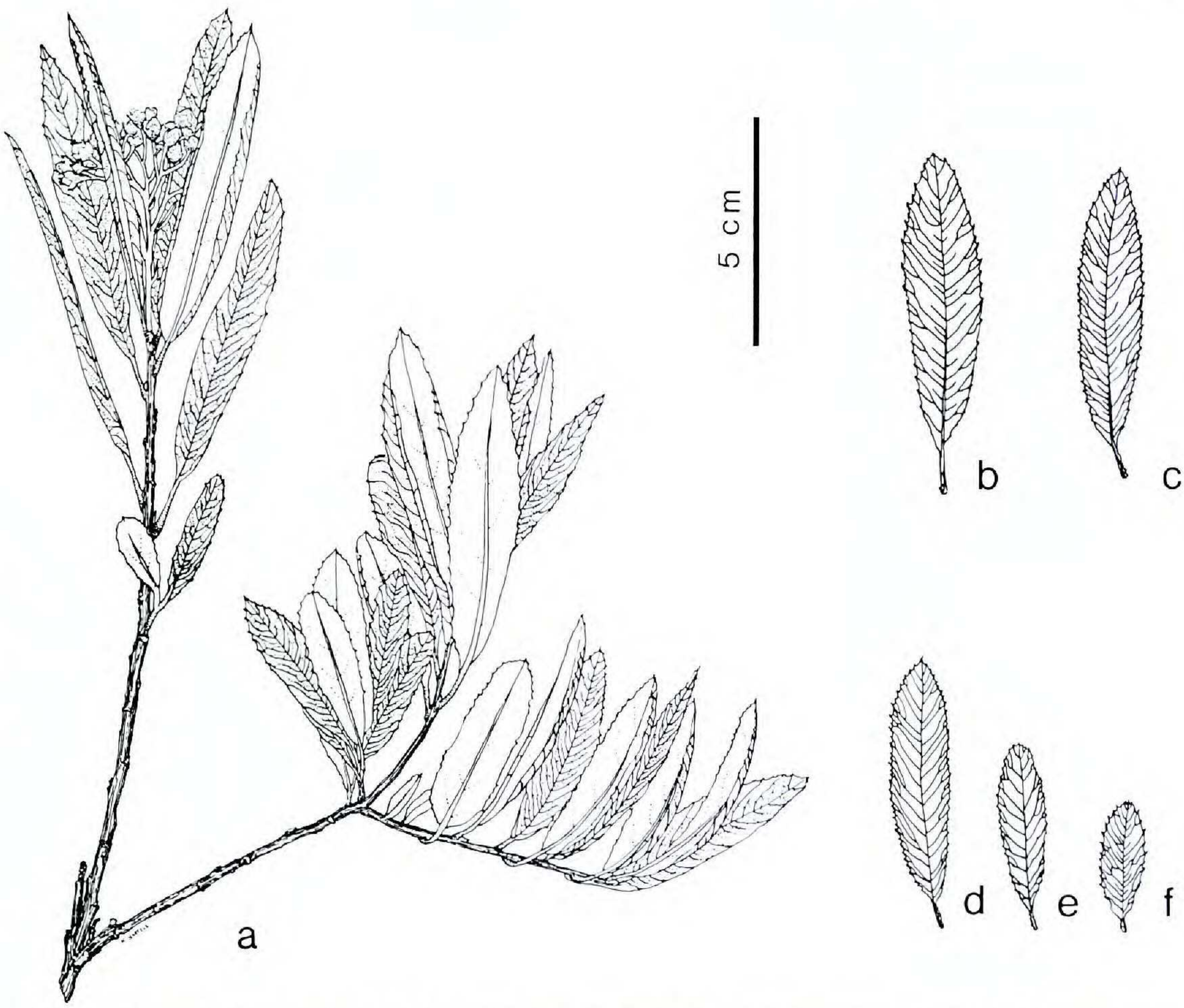


Fig. 8. *Vauquelinia australis*. a.—Young flowering stem showing erect-ascending, bicolored leaves; note recurved margins on some leaves. b-f.—Variation in leaf shape, size. b-d.—Leaves from most populations are broader in distal half (recurved margins are not shown here). *Hess & Wilhelm 4382* from near Nochixtlan, Oaxaca. d-f.—Plants from San Lorenzo near Tehuacan occurring on heavily grazed, limestone hills have much smaller, flat leaf blades. *Hess & Byrne 4671*. Magnifications as indicated in vertical scale.

1 − 6(− 10) m tall; young stems sparsely to closely or densely tomentulose-villous with slender, tightly crinkled, matted hairs 0.1 − 0.3 mm long, tardily glabrate, or persistently tomentulose or canescent with a tight, close covering of coiled hairs; bark smooth, gray to black, developing closely, irregularly plaited on larger trunks. Leaves ascendant to divergent; leaf blades mostly oblong-lanceolate, linear-lanceolate, lanceolate, to variously oblong-elliptical or oblong-ovate, (1.5 −)3.5 − 10(− 15) cm long, (4 −)7 − 15(− 34) mm wide, coriaceous, acute to obtuse, mostly mucronate at tips, abruptly to gradually, often obliquely cuneate to rounded, or subcordate at base, at margins plain, sometimes slightly revolute between serrations, or variously crisped, closely serrulate or crenulate, or partially doubly serrulate or crenulate with 2 − 7(− 10) teeth per cm with serration number depending on development of secondary serra-

tions; serrations ascending to divergent, acute to rounded, 0.1 – 0.5(– 1.5) mm long, gland-tipped, often with additional glands along margins between crenations or serrations, upper serrations margins concave, straight or convex, lower margins concave, straight or sigmoid; lamina often slightly folded along impressed midrib, usually bicolored, initially sparsely to densely, closely villous-tomentulose on both surfaces but this thicker beneath, glabrate or tardily glabrate with persisting, short, crinkled hairs along the impressed midrib or throughout, lustrous or not above, persistently tomentulose to puberulent but vestiture usually much reduced along mid and secondary veins, or nearly to completely glabrate beneath; petioles (1.5 –)4 – 14(– 26) mm long, green-yellow or tinged with red, canaliculate, adaxially winged by decurrent leaf margins, wings usually with glands along margins, variably tomentulose throughout or adaxially; stipules narrowly deltate, 1 – 4 mm long, tomentulose, glabrate, with sessile glands along margins and tips. Compound corymbs small to large, often aggregated at stem tips; pedicels-peduncles densely tomentulose-villous to tomentose, occasionally sparsely pubescent, glabrate; bracts-bracteoles oblong to linear-lanceolate, 1 – 7(– 9) mm long, sparsely to densely tomentulose or puberulent, with sessile glands along margins; hypanthia hemispheric, densely villous-tomentose to sparsely tomentulose, occasionally glabrate, green outside, mostly glabrate-glabrous above a sericeous base inside; sepals thick, broadly ovate, deltate, 1.1 – 2.3 mm long and wide, obtuse to rounded, bluntly mucronate, margins thin, without sessile glands, villous-tomentose to nearly glabrate outside, usually densely villous at least along margins inside; petals oblong-ovate, 2.7 – 5.4 mm long, 2.0 – 3.5 mm wide, rounded to emarginate at tip, broadly cuneate to rounded above a broad claw 0.2 – 0.4 mm long at base, sometime floccose at tip at anthesis but eventually glabrate, recurved and persisting on fruit or not; filaments 2.5 – 5.5 mm long; anthers 0.7 – 1.3 mm long, to 1.8 mm long wet; styles 1 – 2.1 mm long. Mature capsules ovoid, 4.5 – 6.5 mm long, 3.5 – 4.5 mm wide, sericeous; seeds 3.5 – 5 mm long, 0.9 – 1.8 mm wide; embryos 1.6 – 2.7 mm long, 0.8 – 1.2 mm wide.

Vauquelinia californica is distinguished by its oblong-lanceolate to linear, finely crenulate-serrulate-margined, short petiolate leaves, its lack of glands on sepal margins, and its tendency to have marcescent petals. It is here divided into four subspecies ranging from central Arizona southwest to central and southern Baja California, and southwestern New Mexico south to eastern Durango, and eastern and central Coahuila.

KEY TO SUBSPECIES OF *VAUQUELINIA CALIFORNICA*

A. Leaves bicolored, green above, white beneath, (but typically glabrate beneath in central Arizona); Arizona, New Mexico to Baja California, Durango, and central Coahuila.
  B. Leaves lanceolate to oblong-lanceolate or narrowly elliptical, (7)10 – 20(– 32) mm wide, tomentulose, (rarely nearly glabrate beneath, from Maricopa and adjacent Pinal, Gila counties, Arizona), green, lustrous above; central Arizona, and central Baja California. . . . . 2a. *V. californica* subsp. *californica*
  BB. Leaves linear to linear-lanceolate, (4 –)7 – 10(– 13) mm wide, if elliptical then under 4 cm long, persistently white-tomentulose to canescent beneath, slightly puberulent, non-lustrous above.
    C. Leaf-blades (3.5 –)5 – 11(– 14) cm long, (6 –)7 – 12(– 14) mm wide; petioles (4 –)6 – 13(– 22) mm long; leaves permanently white-tomentulose beneath; southwestern Arizona (Ajo Mountains) and northern Baja California .2b. *V. californica* subsp. *sonorensis*
    CC. Leaf-blades (1.5 –)2.0 – 5.5(– 7.7) cm long, 4 – 9(– 13) mm wide; petioles (2 –)4 – 9(– 11) mm long; leaves closely canescent beneath; extreme southwestern Coahuila and northeastern Durango. . . . . 2c. *V. californica* subsp. *retherfordii*
AA. Leaves glabrate, green or yellow-green on both surfaces, occasionally with few trichomes along midvein; extreme southwestern New Mexico, adjacent southeastern Arizona, south to eastern Chihuahua, Durango, and also central Coahuila. . . . . 2d. *V. californica* subsp. *pauciflora*

2a. VAUQUELINIA CALIFORNICA (Torr.) Sarg. subsp. CALIFORNICA Gard. & Forest 2:400. 1889. *Spiraea californica* Torr. in Emory, Notes Mil. Recon. 140. 1848. TYPE: ARIZONA. Gila Co.: high mountains near the Gila, Nov 1846, *Major W. Emory s.n.* (HOLOTYPE: NY!).

Vauquelinia corymbosa Torr. in Emory, Rep. U.S. & Mex. Bound. 2:64. 1859 *non* Humb. & Bonpl.

Vauquelinia torreyi S. Wats. Proc. Amer. Acad. Arts 11:147. 1876.

Multi-stemmed, straggly shrubs to small rounded, obovoid trees 1.2 – 5(– 8) m tall; young stems initially closely tomentulose with tightly crinkled hairs 0.1 – 0.2 mm long, usually persistently canescent with coiled hairs or tardily glabrate. Leaf blades oblong-lanceolate, lanceolate, linear-lanceolate, occasionally oblong-elliptical to oblong-ovate, rarely oblanceolate, (3.5 –)4 – 9(– 15) cm long, (7 –)10 – 20(– 34) mm wide, [leaf-blade length-width ratio (2 –)3 – 6(– 7.4)], coriaceous, 0.23 – 0.27 mm thick, weakly to strongly bicolored, acute, obtuse, mucronate or retuse by dieback at tip, abruptly to gradually, often obliquely cuneate to rounded, truncate, or when very broad, subcordate at base, at margins uniformly, closely crenulate or serrulate or partially doubly crenulate-serrulate with (2 –)3 – 7(– 10) gland-tipped teeth per 1 cm, teeth usually small, rounded, 0.1 – 0.4 mm long, sometimes more serru-

late, with acuminate, divergent to ascending serrations 0.5 – 1.4 mm long, often with additional glands in axils of teeth and along margins between teeth; lamina often slightly folded along midrib, green, yellow-green, with yellow mid and secondary veins, initially villous-tomentulose, mostly glabrate or glabrous, lustrous, except where persistently puberulent along depressed midrib above; usually whitish with a more persistent puberulence of lightly coiled hairs, these sometimes diminishing along secondary veins and along the more glabrate midvein, sometimes nearly glabrescent beneath; petioles (4 –)7 – 15(– 26) mm long, [(0.8 –)0.12 – 0.2(– 0.25) times as long as leaf blades], puberulent-tomentulose with curled hairs throughout or only adaxially, wings broad or very narrow with 2 – 12 pairs of often conspicuous, sessile glands. Compound corymbs 3 – 5(– 12) cm long, 3 – 8(– 13) cm wide; lower peduncles 11 – 65 mm long; pedicels-peduncles puberulent-tomentulose, tardily glabrate; upper bracts-bracteoles lance-subulate, 1 – 5(– 7) mm long, villous-tomentulose with glands along margins; hypanthia 2 – 2.5(– 3) mm long, 2 – 3.7 mm wide, to 4.5 mm wide in fruit, tomentulose-villous, tardily glabrate outside, glabrous below stamens inside; sepals 1.4 – 2.1 mm long, 1.5 – 2.3 mm wide, mucronate, margins thin, lacking sessile glands, puberulent-villous outside, villous particularly along margins inside; petals oblong-obovate, oblong-ovate, 4 – 5 mm long, 2.5 – 3.5 mm wide, often floccose at tip but glabrate, recurving and persisting around fruit; filaments 3 – 5.5 mm long; anthers 0.8 – 1.1 mm long, to 1.5 mm long wet; styles 1.7 – 2 mm long. Capsules 5 – 6.5 mm long, 3.5 – 4.5 mm wide; seeds 4 – 5 mm long, 1.2 – 1.3 mm wide; embryos 2.1 – 2.6 mm long. $n = 15$ (Goldblatt 1976). (figs 1a-b, 9, 10).

Vauquelinia californica subsp. *californica* is characterized by its relatively large, oblong-lanceolate, lanceolate to linear-lanceolate, closely crenulate to doubly crenulate, short-petiolate leaves with leaf blades mostly 4 – 9(– 15) cm long, (7 –)10 – 20(– 34) mm wide, with (2 –)3 – 7 (– 10) teeth per 1 cm margin (fig. 10). In most collections leaves are distinctly bicolored, glabrate or weakly puberulent, at least along the midveins above, and variously, persistently, closely tomentulose to canescent beneath with a vestiture of tightly coiled hairs.

In populations from the Superstition Mountains in northwestern Pinal County, north through the Apache Trail, Fish Creek area in adjacent Maricopa County, and in the Pinal and Mescal Mountains in southern Gila County, leaf blades tend to lose more vestiture on the lower surface, becoming glabrate, or nearly so, except along the midveins. In this character they approach *V. californica* subsp. *pauciflora* that occurs in extreme southeastern Arizona and adjacent New Mexico south into eastern Durango, and central

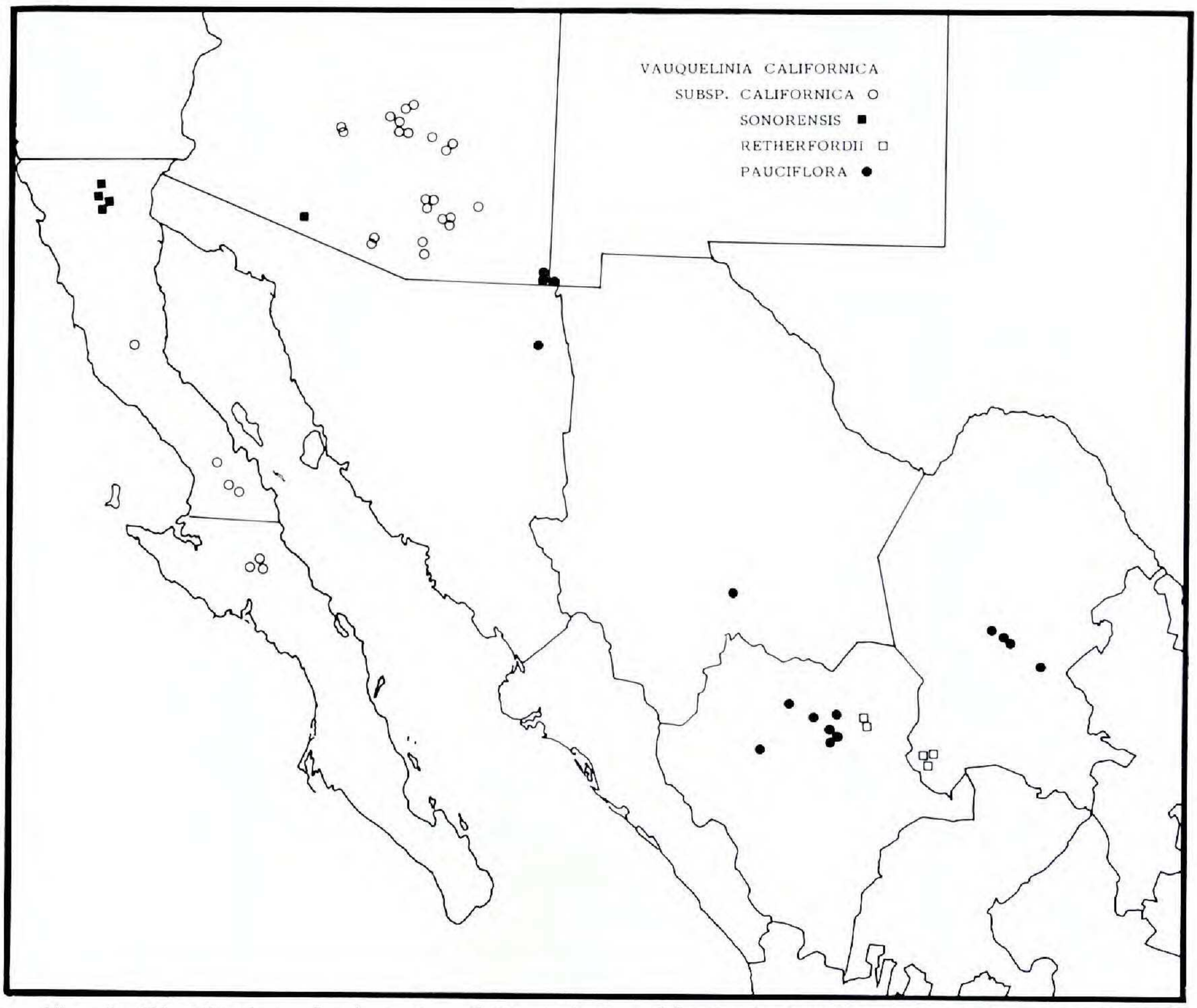


Fig. 9. Distribution of subspecies of *Vauquelinia californica* in México and southwestern United States.

Coahuila. In leaf size, however, they compare more with other populations of *V. c.* subsp. *californica*. Not all specimens are completely glabrate on the lower leaf surface, but retain some vestiture. Thoughts of nomenclaturally recognizing these more glabrate populations were rejected as there appears to be no sharp separation in this vestiture character. Populations from central Baja California, in contrast, tend to have more strongly and persistently vestitured lower leaf surfaces.

The isolated populations of *V. c.* subsp. *californica* exhibit considerable inter- and intra-populational variation. Williams (1971) made statistical analyses of various leaf features of five Arizona populations of *V. c.* subsp. *californica* from the Baboquivari Mountains (Pima County), the Santa Catalina Mountains (Pima County), two areas in the Mescal Mountains (Gila and Pinal counties), and the Superstition Mountains (Pinal County). He found that each population varied in relative leaf length, width, petiole length and, marginal toothing, with populations from the Molino Canyon in the Santa Catalina Mountains averaging the shortest leaves and shortest

petioles (fig. 10e – f), those in Baboquivari Canyon (fig. 1 – n) usually having the narrowest leaves and the least number of marginal teeth per 1 cm, but the differences were not statistically significant. In fig. 10 we show a sample of the wide variation of leaf outline inherent in this taxon, both between and within populations.

Differences also occur in the amount of vestiture retained on stems and inflorescences, in the density and development of marginal leaf toothing (i.e., whether closely or coarsely toothed), and the development of marginal glands. Floral features also undoubtedly vary between populations, but, as flowering material is not available from all populations, these characteristics could not be completely analyzed. Such strong variation is perhaps expected in a taxon whose present interpluvial distribution consists of a series of relictual populations occupying mesic microhabitats in highly isolated ranges.

The type specimen of *V. californica* was apparently collected near the Mescal Mountains in Gila County, Arizona. Emory (1848) noted that during November of 1846, he was "following the course of the Gila River, occasionally forced into the mountains to avoid the canyons." The map accompanying the text indicates that he was at that time on the north side of the river, quite possibly in the Mescal Mountains. There are no other collections known to us from Gila County, Arizona. Williams (1971) studied a population from that general area, only on the south side of the Gila River. He concluded that his collections from the Mescal Mountains were similar to those of Emory's type collection.

Vauquelinia californica subsp. *californica* is locally common in canyons and hillsides, often in rock crevices in both limestone and granite substrates in shrubland communities of the upper Sonoran Desert from just above the desert plains to the lower pinyon-juniper zones (Williams 1971). Populations are known from the Mazatal, Superstition, Pinal, Mescal, Sierra Estrella, Santa Catalina, Rincon, Baboquivari, Santa Rita mountains, and Teran Hills in Maricopa, Gila, Pima, and Cochise counties of south central Arizona, and in the Sierra San Borja, Sierra San Francisco and other scattered ranges of central Baja California, México at elevations from 700 to 1800 m (fig. 9). It occurs in association with a large number of species including *Acacia greggii*, *Agave palmeri*, *A. schottii*, *Aloysia wrightii*, *Artemisia ludoviciana*, *Ayenia pusilla*, *Calliandra humilis*, *Carnegiea gigantea*, *Crossosoma bigelovii*, *Dasylirion wheeleri*, *Dalea formosa*, *Dodonaea viscosa*, *Eriogonum wrightii*, *Erythrina flabelliformis*, *Fouquieria splendens*, *Gutierrezia microcephala*, *Haplopappus laurifolius*, *Krameria parvifolia*, *Opuntia acanthocarpa*, *Opuntia phaeacantha*, *Quercus spp.*, *Porophyllum gracile*, *Simmondsia chinensis*, *Yucca spp.* and species of *Andropogon*, *Aristida*, *Bouteloua*,

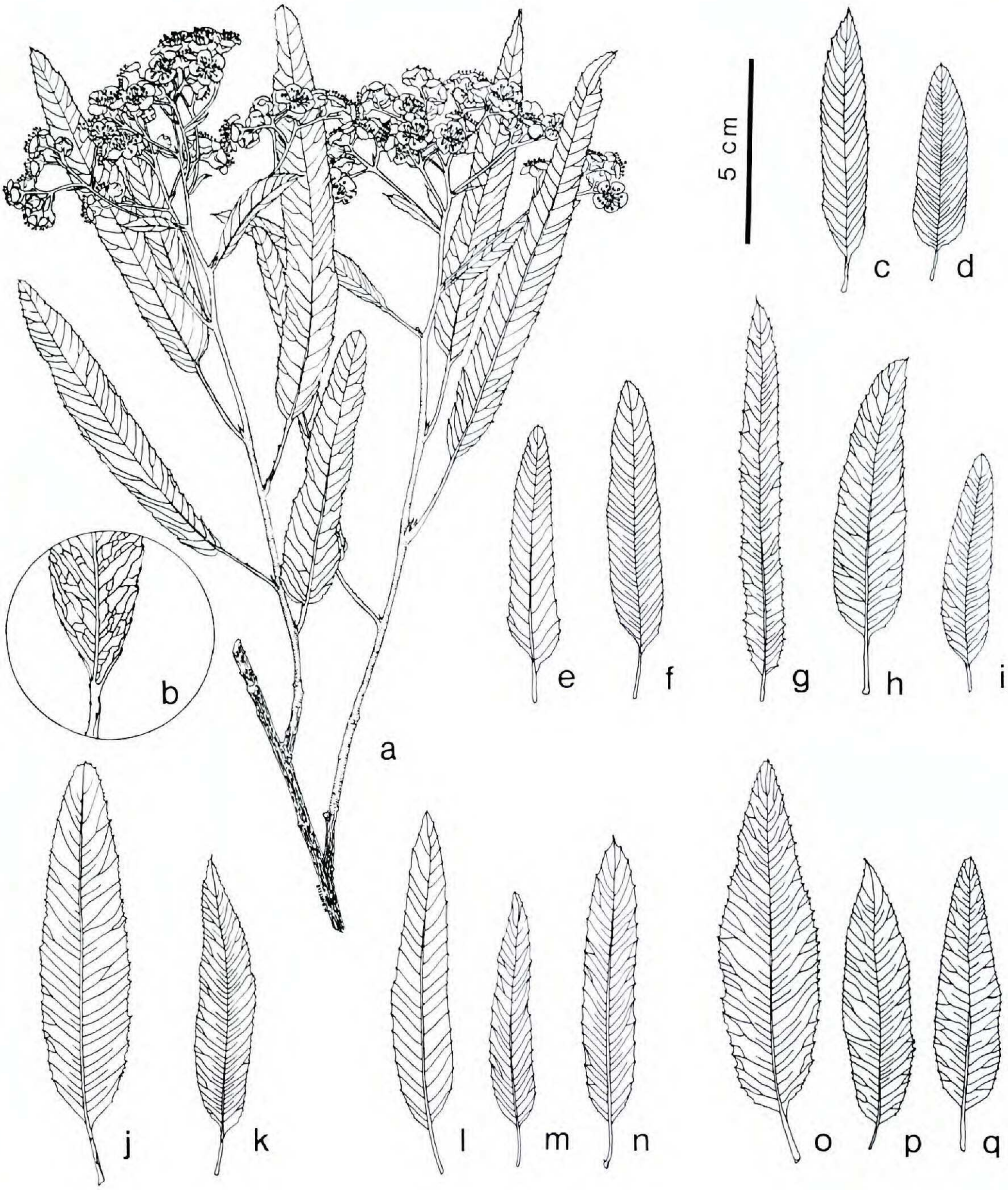


Fig. 10. *Vauquelinia californica* subsp. *californica*. a.—Flowering young stem showing erect-ascending leaves. Note reduced leaves subtending basal peduncles in inflorescences. b.—Leaf base showing glands on petiole wings and continuing up leaf margins. c-q.—Leaf-shape, petiole-length variation throughout range. c-d.—Leaves from Rincon Mountains, SE of Tucson, Pima County, Arizona. c.—*Blumer 3611*. d.—*B. Maguire 11702*. e-i.—Leaves from Santa Catalina Mountains, NE of Tucson, Pima County, Arizona. f.—*M.E. Jones s.n.*. g.—*Thornber 228a*. g-i.—Variation in a single population collection. *Hess & Wilhelm 4256*. j-k.—Variation in leaves from Apache Gap area, E of Phoenix, Maricopa County, Arizona. Both *Hess & Wilhelm 4251*. l-n.—Leaves from Baboquivari Mountains, Pima County, Arizona tend to be narrower, approaching those from the Ajo Mountains. l-m.—*Gilman 127*. n.—*M.E. Jones 24781*. o-q.—Leaves from Sierra Borja in Baja California, México. o.—*Moran 8085*. p.—*Moran 11529*. q.—*Moran 11720*. Magnifications as indicated.

Eragrostis, *Heteropogon*, *Lycurus*, *Muhlenbergia*, *Panicum*, *Tridens*, *Cheilanthes*, *Notholaena*, *Pellaea*, *Selaginella*, *Arabis*, *Echinocereus*, *Euphorbia*, and, *Galium* etc. (Williams 1971).

Representative collections: U.S.A.: Arizona. **Cochise Co.**: S end Teran Hills, at pass W of Allen Flat, road from Cascabel to Willcox T14S R21E S22, 3 Jan 1983, *Yatskievych & Windham 83-18* (ARIZ). **Gila Co.**: Devils Canyon, Pinal Mts., 11 Jul 1926, *Peebles, Harrison & Kearney 2316* (ARIZ); 2 mi E of Coolidge Dam, 2 Jun 1943, *Darrow s.n.* (ARIZ); Mescal Mts., 19 Jul 1976, *Bingham 2366* (ASU). **Maricopa Co.**: Fish Creek, Apache Trail, 21 May 1929, *Eastwood 17386* (CAS, DS-2 sheets, F-3 sheets, NY-2 sheets, US); Near Canyon Lake, Salt River, 21 Jun 1928, *Peebles & Harrison 5538* (ARIZ, US); Apache Trail, 1 mi N of Apache Gap, 3 Jan 1932, *Gillespie 8731* (DS, GH, NY, POM, UC, US). *Pima Co.*: Santa Catalina Mts., Jun 1882, *Pringle s.n.* (A-2 sheets, F-3 sheets, NY-3 sheets, US); Summit, Santa Catalina Mts., Apr 1881, *Lemmon 155* (GH); Sabino Canyon, Santa Catalina Mts., 7 Oct 1894, *Toumey s.n.* (A, NY-2 sheets, US); Manning Trail, Rincon Mts., 11 Apr 1909, *Blumer 3611* (ARIZ, DS, UC); Near Colossal Caves, Rincon Mts., 20 Mar 1930, *McKelvey 516* (GH); Pantano, Mar 1881, *Vasey s.n.* (F, NY, US); Baboquivari Canyon, Baboquivari Mts., 23 Sep 1931, *Gilman 127* (A, ARIZ, DS, GH, NY). **Pinal Co.**: Superstition Mts., 16 Feb 1930, *Fulton & Hastings 6387* (CAS, NY, POM, US); Superior, along stream, 9 Jun 1935, *Whitehead 1354* (US); Sierra Estrella Regional Park, N-facing canyon of Squaw Tit, 20 Oct 1974, *McGill, Franklin, E. & M. Sundell S680* (ASU, RSA).

MÉXICO. **Baja California Norte**: Cliff on S rim of canyon, El Metate 30°11′N, 115°08′W, 29 Dec 1963, *Moran 11447* (DS, SD, UC); Sierra de Borja, upper slope of Cerro el Sauco, 28°46′N, 113°39′W, 27 Mar 1960, *Moran 8085* (DS, SD, UC); N slope of summit of Cerro la Chona, 28°24′N, 113°35′W, 19 Mar 1966, *Moran 12789* (DS, SD); Summit, Cerro la Sandía, 28°24′N, 113°27.5′W, 24 Jan 1964, *Moran 11529* (DS, MEXU, SD, UC). **Baja California Sur**: Sierra San Francisco, summit of Cerro Natividad, 27°28′N, 113°05′W, 24 Feb 1964, *Moran 11748* (DS, LL, SD, UC); Sierra San Francisco, Cerro la Laguna, 27°35′N, 113°02′W, 24 Nov 1976, *Moran 23844* (ARIZ, CAS, SD); Sierra San Francisco, summit of Cerro de la Higuera, 27°31′N, 113°00′W, 21 Feb 1964, *Moran 11720* (ARIZ, DS, RSA, SD, UC, US). **Sonora**: Sierra Verde (probably Baboquivari Mts., Pima Co., Arizona), 17 Jul 1855, *Schott s.n.* (F, GH, MO, NY-2 sheets).

2b. Vauquelinia californica subsp. **sonorensis** Hess & Henrickson subsp. nov.

A ssp. *californica* et *pauciflora* foliis linearibus vel lineari-lanceolatis, infra dense albis, tomentosis et a subsp. *retherfordii* laminis 6 − 12(− 12.5) cm longis, et petiolo 6 − 16(− 22) mm longo differt.

Multi-stemmed shrubs to small trees 1 − 4(− 7) m tall; young stems initially densely white-tomentulose with tightly crinkled hairs 0.1 − 0.2(− 0.3) mm long, vestiture persisting though diminishing in stature, becoming more canescent. Leaf blades linear, narrowly oblong to oblong-lanceolate, (2.5 −)5 − 11(− 15) cm long, (5 −)7 − 12(− 17) mm wide, [length-width ratio (5.5 −)7 − 13(− 15)]; coriaceous, 0.26 − 0.3 mm thick, strongly bicolorous, acute to obtuse, occasionally retuse,

acuminately mucronate at tip, abruptly to gradually, usually obliquely cuneate to nearly rounded at base, at margins thickened, very slightly revolute between teeth, sometimes crisped, uniformly and closely crenulate to serrulate, occasionally partially doubly crenulate with 2 − 3(−6) gland-tipped teeth per 1 cm, crenulations usually low, rounded, (0.1 −)0.2 − 0.4 mm long, sometimes barely evident, or margins more serrulate with acuminate, divergent to ascending teeth 0.6 − 2.5 mm long, often some leaf-blades completely entire; lamina initially villous-tomentulose but soon or tardily glabrate, often with a residual close vestiture of coiled hairs along midrib, generally dull, not lustrous above, persistently white villous-tomentulose with curled hairs forming a layer 0.1 − 0.15 mm thick, though this sometimes diminishing in older leaves, often less densely vestitured along secondary veins with vestiture much reduced along raised yellow midvein beneath; petioles (4 −)6 − 16(−22) mm long, [(0.05 −)0.07 − 0.14(−0.25) times as long as leaf blade], strongly villous-tomentulose throughout or adaxially, 0.8 − 1.2 mm thick, wings thick or thin, with 4 − 6 pair of sessile caducous glands. Compound corymbs 1.5 − 4.5 cm long, 2 − 6.5 cm wide, often clustered at branch tips, rather divergently branched; basal peduncles 11 − 20 mm long; pedicels-peduncles villous to tomentulose with crinkled hairs 0.2 − 0.5 mm long; upper bracts-bracteoles 1 − 5(−9) mm long with glandular margins, densely white villous-tomentose; hypanthia 2 − 2.5 mm long, 3 − 3.5 mm wide, to 4.5 mm wide in fruit, strongly white-villous-tomentulose outside, glabrous inside except at base; sepals 1.3 − 1.8 mm long. 1.6 − 2 mm wide, with yellow, gland-like mucro at tip, margins thin, eglandular, villous-tomentulose outside, generally glabrous except at tip and base inside; petals oblong-ovate, 4 − 5 mm long, 2.4 − 3 mm wide, floccose where exposed in bud, glabrate; filaments 3 − 5 mm long; anthers 1.1 − 1.3 mm long, to 1.8 mm long wet; styles 1.8 − 2.0 mm long. Capsules 5 − 6 mm long, 3.5 − 4 mm wide; seeds 3.5 − 4 mm long, 0.9 − 1.2 mm wide; embryos not seen.

TYPE: ARIZONA. Pima Co.: Organ Pipe National Monument, Arch Canyon, 22 mi s of Why and 12 mi e of visitor center in Ajo Mountains, 31°57′N lat, 112°40′W long, 850 m, 2 Jun 1978, *Hess & Wilhelm 4259* [HOLOTYPE: MOR!; ISOTYPES: (to be distributed)]. (figs. 9, 11a − c).

Vauquelinia californica subsp. *sonorensis* is characterized by its narrow, linear to linear-lanceolate, strongly bicolored leaves with persistently tomentulose lower leaf surfaces, young stems, inflorescences, and hypanthia-calyces (fig. 11a − c).

Subspecies *sonorensis* is restricted to the Ajo Mountains in Pima County, Arizona (in Alamo, Grass, and Arch canyons) and in local areas on the

eastern slopes of the Sierra Juarez in northern Baja California, México (fig. 9). Though separated by some 250 km, the two populations are very similar in most characteristics, though populations in the Sierra Juarez have slightly longer and narrower leaf blades and slightly longer petioles. The populations of *V. c.* subsp. *californica* from central Baja California also have more strongly bicolored leaves, and more densely vestitured stems, inflorescences, etc. than those from Arizona, but the vestiture is not as dense or thick as in subsp. *sonorensis* and the leaves are more lanceolate to oblong-lanceolate, as in other populations of subsp. *californica* in Arizona. Some plants from the adjacent Baboquivari Mountains in Pima County, Arizona have narrow leaves somewhat similar to those of subsp. *sonorensis*, but the plants lack the characteristic dense vestiture on stems, inflorescences, and lower leaf surfaces.

Subspecies *sonorensis* occurs in rhyolite and andesite canyon margins and hillsides, often near ephemeral drainages from 750 – 1500 m, in Arizona with *Simmondsia chinensis, Agave desertii, Aloysia wrightii, Artemisia ludoviciana, Celtis reticulata, Dodonaea viscosa, Eriogonum fasciculatum, E. wrightii, Fouquieria splendens, Gutierrezia microcephalum, Haplopappus laricifolius, Janusia gracilis, Juniperus monosperma, Opuntia phaeacantha, Quercus ajoensis, Sapindus saponaria*, and species of *Aristida, Bouteloua, Muhlenbergia, Stipa, Tridens, Cheilanthes, Notholaena, Pellaea*, and *Selaginella*, and in Baja California in the ecotone between the Sonoran Desert woodland the pinyon wooodlands with *Agave desertii, Brickellia arguta, Eriogonum fasciculatum, Haplopappus cuneatus, Keckiella antirrhinoides, Pinus quadrifolia, Quercus turbinella*, and species of *Berberis, Opuntia, Echinocereus, Stipa, Arabis, and Ferocactus*.

Representative collections: U.S.A.: ARIZONA. **Pima Co.**: Canyons of Ajo Mts., 2 Apr 1944; *Clark 11575* (GH, TEX); Ajo Mountains, Organ Pipe Cactus National Monument, main fork of Alamo Canyon, 15 Aug 1952, *Tucker 2427* (CAS, UC); Ajo Mountains, Alamo Canyon, 19 Apr 1942, *Cooper 597* (ARIZ, ASU); Summit of Bull Pasture Trail, Organ Pipe National Monument, 11 Oct 1976, *Cummins s.n.* (ARIZ).

MÉXICO: **Baja California Norte**: 18 rd mi SSE of La Rumarosa near Rancho San Ignacio (La Milla) in canyon N of Cerro la Milla, 27 Jul 1985, *Henrickson 20281* (TEX); El Torundo, 32°25′N, 115°53′W, 16 Mar 1968, *Moran 14825* (SD); Head of Cantilles Canyon, 32°18′N, 115°55′W, 3 Apr 1966, *Beauchamp s.n.* (SD); E side of Sierra Juarez, Tajo Cañon, 32°16′N, 115°55′W, 9 Sep 1957, *Moran 6105* (DS, RSA, SD); Sierra Juarez, Casimiro, NE of El Topo, 32°18′N, 115°54′W, 27 Sep 1970, *Moran 18190* (SD, DS, RSA).

2c. VAUQUELINIA CALIFORNICA subsp. **retherfordii** (I.M. Johnston) Hess & Henrickson, stat. et comb. nov. *Vauquelinia retherfordii* I.M. Johnston. J. Arnold Arbor. 24:234. 1943. TYPE: México. COAHUILA: Sierra Jimulco, 11 km ne of Jimulco, 28 Jun 1941, *L.R. Stanford, K.L. Retherford, & R.D. Northcraft 87* (HOLOTYPE: GH!; ISOTYPES: ARIZ! DS! MO! NY! UC!).

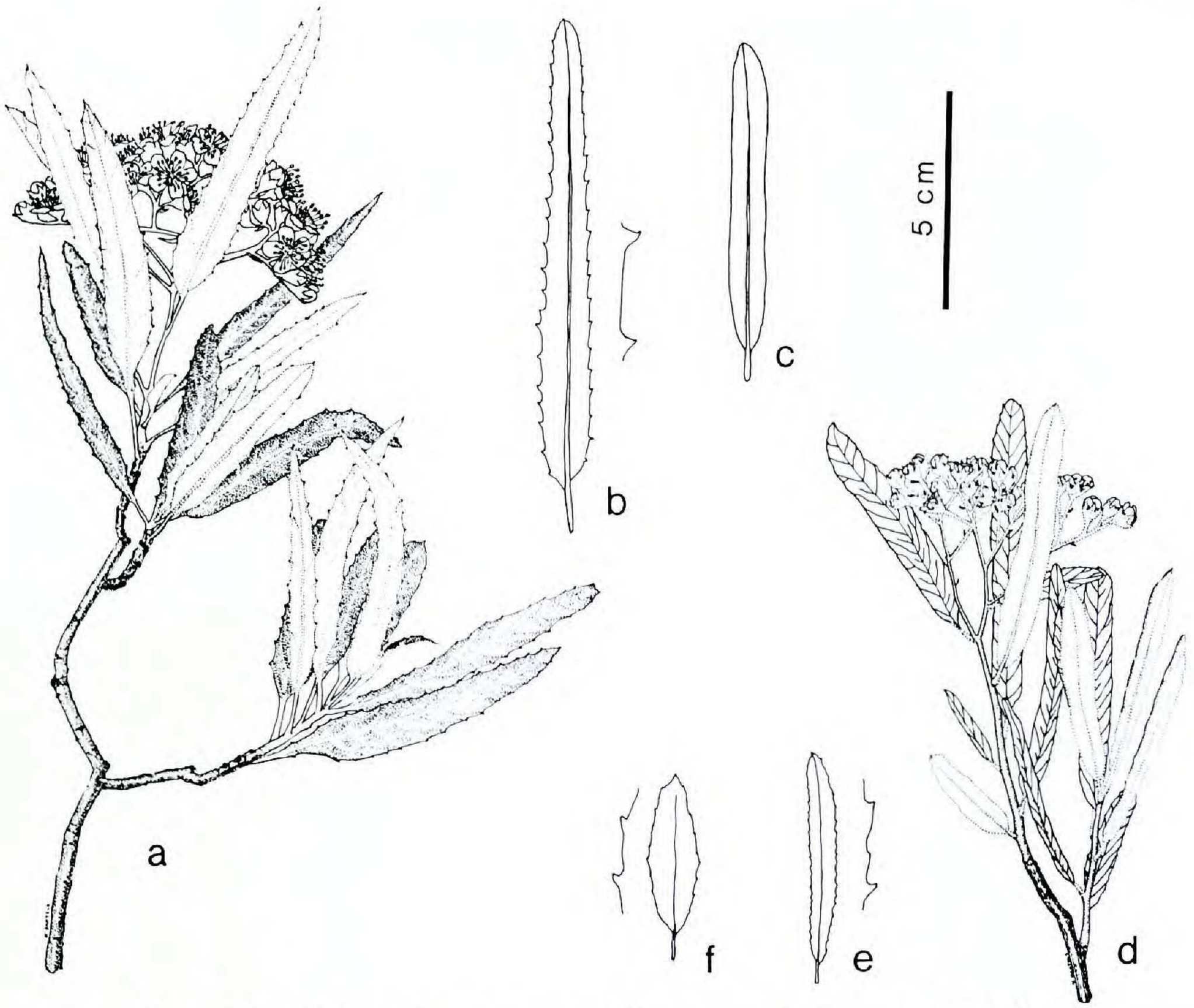


Fig. 11. *Vauquelinia californica* subsp. *sonorensis* and *V. c.* subsp. *retherfordii*. a-c. *V. c.* subsp. *sonorensis*. All collections from the Ajo Mountains, Pima County, Arizona. a.—Young stem showing characteristic oblong-lanceolate, bicolored leaves and flowers. *Hess & Wilhelm 4259*. b.—Leaf outline showing coarse toothing (toothing expanded in outline at right). *Harbison 45544*. c.—Occasional plants have some entire leaves. *Hess & Wilhelm 4259*. d-f.—*V. c.* subsp. *retherfordii*. d.—Young stem showing narrow oblong, bicolored leaves, flowers. Collection from the Sierra de Jimulco, Coahuila, México. *M.C. Johnston et al. 11492*. e-f.—Leaf outlines with marginal toothing expanded. e.—From type specimen from Sierra Jimulco, Coahuila, México. *Stanford et al. 87*. f.—An abnormal narrowly ovate leaf from collection in Sierra Rosario in Durango, México. *Wendt et al. 10021*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

Multi-stemmed shrubs to ovoid small trees $2-4(-6)$ m tall; young stems closely, usually persistently canescent with tightly coiled, white hairs $0.1(-0.2)$ mm long, with vestiture usually not completely covering stems, tardily glabrate. Leaf blades linear-lanceolate, narrowly oblong, oblong-elliptical, in one collection, broadly oblong-ovate, $(1.5-)2-5.5(-7.7)$ cm long, $4-9(-15)$ mm wide, [length-width ratio $(2-)5-9$], slightly coriaceous, $0.22-0.27$ mm thick, obtuse to acute, mucronate at tip, abruptly to gradually, usually obliquely cuneate at base, at margins usually somewhat revolute or variously coarsely crisped, closely crenulate-serrulate or partially doubly crenulate with $3-5(-8)$ gland-

tipped teeth per 1 cm, teeth usually low, rounded, (0.1 −)0.2 − 0.4 mm long, sometimes scarcely evident, rarely absent in some leaves, occasionally serrulate or distally serrulate with ascending, acute, teeth 1.0 − 1.2 mm long, sometimes with glands in axils of teeth or on margins between teeth; lamina green, not lustrous, initially sparsely, closely puberulent with coiled hairs, usually glabrate with a yellow, sunken midrib above, grayish, persistently very closely canescent except along raised yellow or basally reddish midrib beneath; petioles (2 −)4 − 9(− 11) mm long, [(0.05 −)0.1 − 0.2(− 0.25) times as long as leaf-blade] sparsely to densely canescent throughout, 0.8 − 1.1 mm thick, wings narrow or tapering, sometimes with few caducous glands along margins. Compound corymbs 1.2 − 5 cm long, 1.5 − 7 cm wide, often aggregated; basal peduncles 4 − 18 mm long; pedicels-peduncles canescent to tightly tomentulose with hairs to 0.1 − 0.2 mm long, very tardily glabrate; upper bracts-bracteoles subulate, 0.7 − 2.2 mm long, marginal glands not evident; hypanthia 1.7 − 2.2 mm long, 2.5 − 3.0 mm wide, to 3.8 mm wide in fruit, puberulent with coiled hairs outside, sericeous to partially glabrous inside; sepals 1.1 − 1.9 mm long, 1.4 − 1.8(− 2.2) mm wide, mucronate, at margins thin, without glands, puberulent outside, sericeous to partially glabrous, densely villous along margins inside; petals oblong-obovate, oblong-ovate, 2.7 − 4.4 mm long. 2 − 2.7(− 3.2) mm wide; filaments 2.7 − 5.0 mm long, anthers 0.7 − 0.9 mm long, to 1.2 mm long wet; styles 1.8 − 2.0 mm long. Capsules 5 − 6.5 mm long, 3.5 − 4.5 mm wide; seeds 4 − 5 mm long, to 1.3 − 1.8 mm wide; embryos 2 − 2.2 mm long, 1.1 mm wide (fig. 11d − f).

Vauquelinia californica subsp. *retherfordii* is characterized by its generally small, narrow, bicolored leaves that are dull, not lustrous, green, sparsely puberulent to glabrous above and very closely white-canescent with a vestiture of tightly curled hairs (fig. 2b) except along the midribs beneath. Marginal serrations or crenulations are low, variable in development, often quite reduced, and leaf blades are usually slightly revolute between the teeth. Young stems have similar, low, tightly crinkled hairs that do not completely cover stems, but reveal the underlying red-brown coloration.

The taxon is known from the Sierra Jimulco in southwestern Coahuila and the Sierra del Rosario in adjacent northeastern Durango (fig. 9). The two populations are separated by about 75 km and are similar in most characteristics, including vestiture and petiole length. They exhibit some differences in leaf shape, those from the Sierra Jimulco having narrow, more linear-lanceolate leaves with revolute margins and relatively few teeth (fig. 11e) while plants from the Sierra del Rosario tend to have broader, more elliptical leaves with more distinct serrations along their more plain

margins, and the leaf blades tend to be more folded along the midvein (fig. 11f). Leaves of plants from the Sierra Jimulco are somewhat similar to those of subsp. *sonorensis*, but they are smaller, only 2 – 6 cm long, the shortest in the genus, 4 – 8 mm wide, whereas those of subsp. *sonorensis* are 5 – 12 cm long and 6 – 12 mm wide. The patterns of vestiture are also similar in the two taxa, except vestiture of subsp. *retherfordii* is less dense and of lower stature than that of subsp. *sonorensis*. Also, subsp. *sonorensis* occurs at lower elevations, below 1500 m on igneous-derived soils, while subsp. *retherfordii* occurs above 1800 m on limestone soils.

Vauquelinia californica subsp. *retherfordii* occurs in izotal to chaparral scrub in limestone canyons and hillsides from 1800 to 3100 m elevation in association with *Garrya*, *Lindleya*, *Rhus virens*, *Arctostaphylos*, *Quercus*, *Yucca canerosana*, *Agave macroculmis*, *A. parrasana*, and *Fouquieria splendens*.

Representative collections: MÉXICO. **Coahuila**: Sierra de Jimulco, to 3 km N of Mina San José, near 25°06′N, 103°13′W, 27 Sep 1972, *Chiang, Wendt & M.C. Johnston 9548b* (LL); Sierra de Jimulco, N-facing cliffs, near 25°11′N, 103°12′W, 27 Jun 1973, *M.C. Johnston, Wendt & Chiang 11492* (LL); 27 (air) mi SE of Torreon, N side of Sierra Jimulco, S of La Rosita, 25°13′N, 103°13′W, *Henrickson 15874* (TEX). **Durango**: N end of Sierra del Rosario, SW of Mapimí, 25°43′N, 103°57′W, 2 Nov 1972, *Wendt, Chiang & M.C. Johnston 10027* (LL); NW third of Sierra Rosario, near 25°42′N, 103°57′W, 25 Jun 1973, *M. C. Johnston, Chiang & Wendt 11470* (LL).

2d. Vauquelinia californica (Torr.) Sarg. subsp. **pauciflora** (Standl). Hess & Henrickson stat. et comb. non. *Vauquelinia pauciflora* Standl. Proc. Biol. Soc. Wash. 31:132. 1918. Type: MÉXICO. Sonora: Guadalupe Canyon, ne Sonora [probably from southern Cochise Co., Arizona], 3 Oct 1893, *Mearns 2535* (holotype: US!).

Multi- to single-stemmed shrubs, small trees 2 – 4(– 8) m tall; young stems initially closely to loosely tomentulose-villous with tightly crinkled hairs 0.1 – 0.2 mm long, tardily glabrate with persisting short curled puberulence or glabrate. Leaf blades lanceolate, oblong-lanceolate to elliptic, oblong-elliptic, occasionally oblong-ovate, rarely oblanceolate, (2.2 –)3 – 7.5(– 9) cm long, (6 –)8 – 14(– 20) mm wide, [leaf blade length-width ratio (2.8 –)3.5 – 6.5(– 8.6)], coriaceous, 0.2 – 0.3 mm thick, acute, obtuse, rounded or emarginate by dieback, mucronate at tip, abruptly, usually obliquely cuneate to subrounded, occasionally rounded at base, at margins uniformly, closely crenulate, serrulate or doubly crenulate, serrulate with (2 –)4 – 8(– 9) gland-tipped teeth per 1 cm, crenulations low, rounded, (0.1 –)0.2 – 0.4 mm long, sometimes scarcely evident, occasionally more acute, ascending 0.5 – 0.7 mm long, often with dark glands in axils or along margins between teeth; lamina green to yellow-green with yellow mid-secondary veins, glabrate or puberulent

along lower midvein, dull green above, more yellow- to gray-green, with raised yellow, rarely reddish midveins, glabrous or persistently puberulent along midrib beneath; petioles (1.5 −)4 − 16(− 22) mm long, [0.06 −)0.1 − 0.25(− 0.34) times as long as leaf-blades], puberulent throughout or adaxially, occasionally glabrate, 0.85 − 1.2(− 1.4) mm thick, wings thin or broad and tapering with 2 − 7 pair of caducous glands along margins. Compound corymbs 1.5 − 5 cm long, 1.7 − 7 cm wide; lower peduncles 7 − 25 mm long; pedicels-peduncles closely puberulent with coiled hairs to 0.1 mm long to glabrate; bracts-bracteoles lanceolate to subulate, 1.5 − 8 mm long, glandular along margins; hypanthia 1.5 − 2.5 mm long, 2.5 − 3.3 mm wide, to 4.5 mm wide in fruit, puberulent, tardily glabrate outside, glabrous to sericeous inside; sepals 1.1 − 2.2 mm long, 1.4 − 2.0 mm wide, mucronate, margins thin, without sessile glands, puberulent to glabrate outside, villous throughout or only along margins and tip inside; petals oblong-obovate, oblong-ovate to broadly elliptic, 3.4 − 5.4 mm long, 2.4 − 3.4 mm wide, persistent or not; filaments (2.5 −)3 − 6 mm long; anthers 0.8 − 1.1 mm long, to 1.6 mm long wet; styles 1.7 − 2 mm long. Capsules (4.5 −)5 − 6 mm long, 3.5 − 4(− 4.5) mm wide; seeds 3.8 − 5.0 mm long, 1.1 − 1.4 mm wide; embryos 1.8 − 2.4 mm long, 0.9 − 1.2 mm wide. (figs. 9, 12).

Vauquelinia californica subsp. *pauciflora* is characterized by its mostly lanceolate, oblong-lanceolate, crenulate- to serrulate-margined, concolorous leaf blades that tend not to be lustrous above and tend to be glabrate except along the lower midvein on both surfaces and the petioles. The taxon is easily separable from subspecies *sonorensis* and *retherfordii*, as the latter two subspecies at all times have permanently concolorous, more linear, linear-lanceolate leaf blades. Its separation from subsp. *californica* is more difficult, as leaves of individuals of subsp. *californica*, particularly those from populations north and east and in the Superstition Mountains in Pinal and neighboring Maricopa and Gila counties, also tend to become completely glabrate in time, and in this glabrescent characteristic, are identical with subsp. *pauciflora*. Those glabrescent-leaved populations of subsp. *californica*, however, tend to have larger leaves and blend directly into populations of subsp. *californica* with canescent lower leaf surfaces that also tend to have larger leaves than in subsp. *pauciflora*. The factor that prompts us to recognize the taxon *pauciflora* is that the northernmost populations of subsp. *pauciflora* in extreme southeastern Arizona and adjacent New México have relatively small, thickened leaves and small inflorescences (fig. 12a − b), perhaps reflecting the aridity of their habitat, and in this character state are easily distinguished from adjacent populations of subsp. *californica*. Populations of subsp. *pauciflora* from Durango

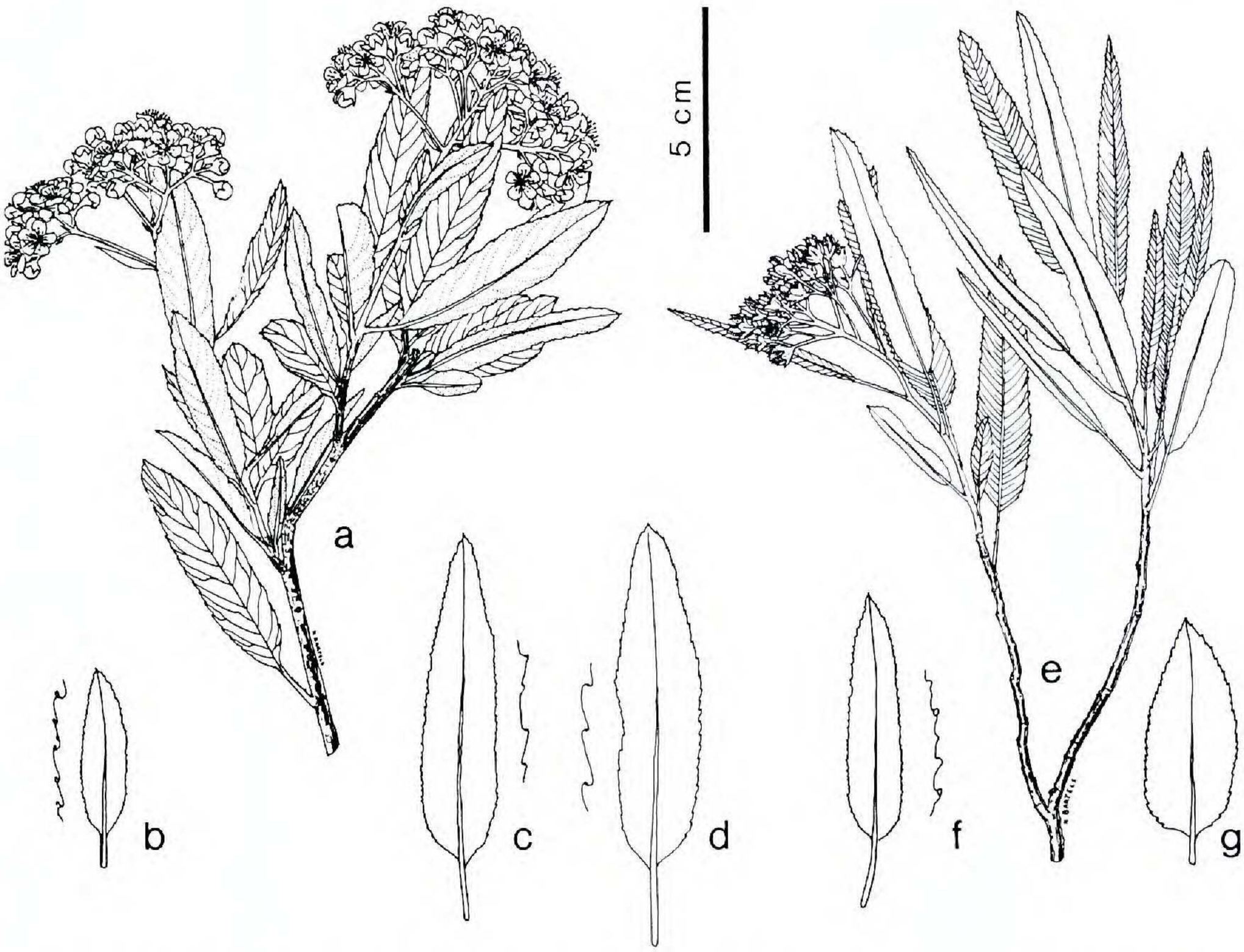


Fig. 12. *Vauquelinia californica* subsp. *pauciflora*. a.—Young stem showing leaves and inflorescences. Collection from extreme southeastern Cochise County, Arizona. *Hess & Wilhelm 4261*. b-d.—Leaf outlines with expanded portions of margins showing leaf variation. b.—Plants from Arizona have very small relatively thickened leaves. *Hess & Wilhelm 4261*. c-d.—Plants from eastern Durango have much larger leaves and are similar to glabrate populations of *V. c.* subsp. *californica*. c.—From near Palmito, *Hess & Wilhelm 4322*. d.—From 42 km S of La Zarca, *M.C. Johnston et al 11436*. e.—Young stem of collection from central Coahuila near Cuatro Ciénegas showing more oblong-lanceolate leaves. *Pinkava et al 6020*. f.—Leaf of same Pinkava collection with expanded margin. g.—Outline of broadly oblong-ovate leaf with short petiole from upper slopes of Sierra San Marcos considered as possible intergrade with *V. corymbosa* subsp. *karwinskyi*. *Engard & Getz 343*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

occurring in grassland-scrub habitats, however, have larger, slightly thinner leaves than the Arizona-New México populations (fig. 12c−d), and in this character approach subsp. *californica*. Perhaps the glabrous-leaved populations of subsp. *californica* should also be included in subsp. *pauciflora*, but this, we feel, would put too much weight on the single vestiture character. Whether the glabrescent leaf character state present in the northern populations of subsp. *californica* is derived from the southern populations here placed in subsp. *pauciflora* or is an idependently derived character state is unknown. Our classification represents a workable, perhaps artificial, division between these closely related taxa and implies

that the northern glabrate populations of *V. c.* subsp. *californica* have been independently derived.

Over its range there is an expected amount of variation. As noted above, populations from the arid desertic hillsides in Arizona and New Mexico tend to have shorter, narrower, thicker leaf-blades and shorter petioles than those from grassland habitats in eastern Chihuahua and Durango. The Chihuahua and Durango specimens are also more consistently glabrous. Some collections from Coahuila show intergradation with subspecies of *V. corymbosa*. The collection of *Engard & Getz 342* (fig. 12g) from the Sierra San Marcos southeast of Cuatro Ciénegas has more oblong-ovate leaves to 20 mm wide and very short, thickened, reddish petioles, and in those characters, approaches *V. corymbosa* subsp. *karwinskyi* and subsp. *latifolia* of nearby Tamaulipas. In its fine marginal toothing, however, the Engard & Getz collection is more similar to other collections of subsp. *pauciflora* from the area. There is very strong and evident intergradation of subsp. *pauciflora* with *V. corymbosa* subsp. *heterodon* from the nearby Sierra Paila in south-central Coahuila as is discussed under the latter taxon. These collections tend to have the long leaf-blades and long petioles of subsp. *heterodon*, combined with the tighter marginal toothing of subsp. *pauciflora*.

The type collection of subsp. *pauciflora* was made by Mearns in 1893 during the Mexican-United States Boundary survey. The label states "Guadalupe Canyon, Sonora", but the collection is doubtfully from México, as suitable rocky limestone habitats are lacking south of the border (Wells and Johnson 1964).

As circumscribed subsp. *pauciflora* ranges from Cochise County, Arizona and adjacent Hidalgo County, New Mexico, with isolated populations in northeastern Sonora, southern Chihuahua, and northern Durango, and in central Coahuila in the mountains around Cuatro Ciénegas and southward, where it occurs in mostly semi-arid to arid limestone hillsides from 1400 – 2300 m elevation (fig. 9). Its wide distribution on both sides of the Chihuahuan Desert indicates that it probably occurred throughout the Chihuahuan Desert region during the Holocene. It occurs in arid chaparral-desert scrub in association in limestone substrates with *Mortonia scabrella*, *Parthenium incanum*, *Fouquieria splendens*, *Nolina microcarpa*, *Agave palmeri*, *Trichostema arizonicum*, *Juniperus monosperma*, *Juniperus spp.*, *Prosopis glandulosa*, *Rhus virens*, *Purshia mexicana*, *Mimosa biuncifera*, and species of *Berberis*, *Ephedra*, *Quercus*, *Agave*, and *Yucca*.

Representative collections: U.S.A: Arizona. **Cochise Co.**: Hill, 5 mi NW of Guadalupe Canyon, 27 May 1952, *Blakley & McCleary 1262* (ASU); 24 mi E of Douglas, Guadalupe Canyon, 13 Jun 1970, *Hess 2667* (MOR); same area, 23 Apr 1975, *Hess & Stickney 3440* (MOR); same area, 3 Jun 1978, *Hess & Wilhelm 4261* (MOR). New Mexico: **Hidalgo**

Co.: near New Mexico line, 6 Oct 1944, *Hershey 3377* (GH); 29 mi E of Douglas, Guadalupe Canyon, 25 Apr 1975, *Hess & Stickney 3445* (MOR).

MÉXICO: **Chihuahua**: 9.5 km S of Valle de Zargoza on road to Hidalgo de Parrál, 27°24′N, 105°49′W, 21 Jun 1973, *M.C. Johnston, Wendt & Chiang 11424* (LL). *Coahuila*: 8 km W of Cuatro Ciénegas, slopes of Sierra de la Madera, 26°58′N, 102°08′W, 5 Aug 1973, *M.C. Johnston, Chiang & Morafka 12081a* (LL); Sierra de San Marcos, opposite Los Fresnos, 4 – 5 Apr 1969, *Pinkava et al. 6020* (ASU, NY); Top of Sierra San Marcos, W of Reynolds Mine Headquarters; 12 Jul 1974, *Engard & Getz 342* (ARIZ, LL). **Durango**: Indé, Jun 1927, *Reko 5145* (F, US); W slope of Sierra de Zarca, 15 mi E of Palmito Dam, 19 Sep 1938, *I.M. Johnston 7771* (GH); 12 mi W of La Zarca towards El Palmito, 28 Jul 1959, *Straw & Forman 1723* (MICH, RSA, UC); 13 Mi E of La Zarca, 17 Jun 1955, *M.C. Johnston 2596a* (MICH, TEX-2 sheets); 42 km S of La Zarca, 10.5 km N of Alamilla de Galeana, 25°27′N, 104°36′W, 22 Jun 1973, *M.C. Johnston, Wendt & Chiang 11436* (LL); 14.9 rd mi NW Los Herreras in Cañon de Potrero, 25°15′N, 105°39′W, 10 Jul 1983, *Corral D. & Worthington 11024* (MO). **Sonora**: Cañon de la Bota, N end of Sierra el Tigre, ca 34 air km ESE of Esqueda, 30°36′N, 109°13′W; 31 Jan 1982, *VanDevender, Yatskievych 82-60* (ARIZ).

3. Vauquelinia corymbosa Humboldt & Bonpland

Multi-stemmed shrubs to single-trunked trees 1.5 – 7(– 10) m tall; young stems initially tomentulose with tightly crinkled hairs, soon to tardily glabrate, sometimes with persistent, close puberulence of coiled hairs that fall with epidermis; bark gray, dark gray, smooth, often plaited in vertical strips on larger trunks. Leaves erect-ascending or drooping on short to elongate petioles; leaf-blades linear to broadly ovate, (2.4 –)3 – 12(– 17) cm long, (3 –)10 – 40(– 65) mm wide, subcoriaceous to rigidly coriaceous, acute to rounded, mucronate at tip, obliquely cuneate to truncate-subcordate with margins decurrent along adaxial petiole at base, at margins plain to variously crisped, variably serrate, doubly serrate to serrulate with 3 – 21, mostly acute-acuminate, ascending to divergent serrations per 5 cm, their number depending on the extent of development of secondary serrations, serrations often variable among leaves of a shoot, upper serration margins variably concave, straight or convex, lower margins concave, straight or sigmoid, corneous, usually terminating with a distinct, sessile, terminal, caducous gland, similar glands sometimes present in axils of teeth and along margins between teeth, gland bases often dark, persisting; lamina densely villous-tomentose when young, glabrate, green, yellow-green, lustrous, with slightly impressed, yellowish midvein above, glabrate, subglabrate, sometimes developing local accumulations of wax, more yellow- to gray-green, with yellowish midvein raised, secondary and smaller veins at least visible beneath; petioles (4 –)10 – 40(– 65) mm long, thick or slender, yellow-green or tinged with red, canaliculate, adaxially winged by decurrent leaf margins

in distal one-half or two-thirds, wing margins with scattered sessile, caducous glands; stipules narrowly deltate, 0.5 – 1 mm long, glabrous to tardily glabrate, obscurely gland-margined. Compound corymbs 2 – 7(– 10) cm long, 2.5 – 9(– 10.5) cm wide, often aggregated at stem tips, each terminating a lateral branch; pedicels-peduncles yellow-green to reddish-brown below, puberulent, floccose to glabrate; hypanthia obconic to hemispheric, densely villous with crinkled hairs in bud, variously glabrescent, often lustrous outside, usually glabrous, nectariferous below filaments, sericeous around ovary inside; sepals broadly ovate, deltate, 1.2 – 2.5(– 3.5) mm long, 1.5 – 2(– 2.5) mm wide at base, strongly mucronate, margins thin, often with sessile glands, variously villous inside with hairs usually showing along margins; petals oblong-ovate, oblong-obovate, (2.4 –)4 – 5.6 mm long, 1.8 – 4 mm wide, rounded to occasionally retuse at tip, broadly cuneate to rounded, often above a broad claw 0.2 – 0.5 mm long at base, initially villous-tomentulose where exposed in bud but usually glabrate, sometimes loosely floccose at tip at anthesis; stamens 18 – 20; filaments 2.7 – 6.5 mm long; anthers 0.6 – 1.1 mm long, to 1.5 mm long wet; styles 1.3 – 2.4 mm long. Capsules 4.5 – 7.5 mm long, 3 – 6.5 mm wide; seeds (3.5 –)4 – 6 mm long, 1 – 1.6 mm wide (including wing); embryos 1.6 – 3 mm long, (0.7 –)1 – 1.3 mm wide (figs. 14 – 19).

With six subspecies occurring from Texas, Coahuila and south along the Sierra Madre Oriental to Hidalgo (fig. 13).

KEY TO SUBSPECIES OF *VAUQUELINIA CORYMBOSA*

A. Petioles mostly 25 – 55(– 65) mm long.
  B. Leaf-blades oblong-lanceolate, oblong-elliptical, oblong-ovate, to broadly ovate, (4 –)6 – 10(– 11.5) cm long, serrate to partially doubly serrate with 6 – 10(– 14) teeth per 5 cm; Hidalgo to Querétaro . . . . . 3a. *V. corymbosa* subsp. *corymbosa*
  BB. Leaf-blades lanceolate to oblong-lanceolate, mostly 7 – 14(– 17) cm long, coarsely, doubly serrulate with (6 –)8 – 19(– 21) teeth per 5 cm; eastern Coahuila and adjacent Nuevo León . . . . . 3b. *V. corymbosa* subsp. *heterodon*

AA. Petioles mostly 5 – 28 mm long, rarely longer.
  B. Leaves narrowly linear, oblong-linear, 7 – 13(– 17) cm long, (3 –)5 – 9(– 12) mm wide, strongly serrate to partially doubly serrate; Texas, eastern Chihuahua to central Coahuila. . . . . 3c. *V. corymbosa* subsp. *angustifolia*
  BB. Leaves oblong-lanceolate to ovate, broader in the lower half, (1.2 –)3 – 9(– 13) cm long, 10 – 45(– 65) mm wide; San Luis Potosí, Nuevo León to Tamaulipas.
    C. Leaves oblong-lanceolate, oblong-elliptical, oblong-ovate or ovate, 3 – 9(– 13) cm long, 10 – 25(– 36) mm wide, not

glaucous, moderately coriaceous; petioles 5 – 24(– 34) mm long, moderately thin, 0.7 – 1.5(– 2) mm wide, winged distally or nearly to base by decurrent leaf margins; San Luis Potosí, western Tamaulipas to Nuevo León.

D. Inflorescence, young stems, and petioles usually glabrate; petioles (8 –)12 – 18(– 34) mm long, winged in distal half; leaf-blades (4 –)5 – 19(– 13) cm long; San Luis Potosí to western Tamaulipas. . . 3d. *V. corymbosa* subsp. *karwinskyi*

DD. Inflorescence, young stems, petioles persistently puberulent; petioles 4 – 9(– 13) mm long, winged to near the base; leaf-blades 3 – 5 (rarely to 7) cm long; eastern Coahuila to Nuevo León. 3e. *V. corymbosa* subsp. *saltilloensis*

CC. Leaves broadly oblong-ovate to broadly ovate, (3 –) 5 – 8(– 12.5) cm long, (15 –)22 – 40(– 65) mm wide, glaucous, strongly coriaceous; petioles stout, (7 –)10 – 15(– 18) mm long, 1.2 – 2.5 mm thick, usually tinged with red, not winged by decurrent leaf markings; western Tamaulipas. . . . . 3f. *V. corymbosa* subsp. *latifolia*

3a. VAUQUELINIA CORYMBOSA Humb. & Bonpl. subsp. CORYMBOSA, Pl. Aequin. 1(6):140, pl. 40. 1807. TYPE: MÉXICO. HIDALGO: juxta Actopan, Aug 1803, *Humboldt & Bonpland s.n.* (HOLOTYPE: P – microfiche!; ISOTYPE: F! – fragment from P).

Small rounded trees to multi-stemmed shrubs 2 – 6(– 8) m tall; young stems initially tomentulose, soon or rarely tardily glabrate. Leaves ascending or drooping; leaf-blades oblong-lanceolate to narrowly lanceolate to narrowly elliptical, oblong, narrowly oblong, oblong-ovate, broadly ovate, (4.2 –)6 – 10(– 11.5)[– 12.7] cm long, (8 –)11 – 28(– 43) mm wide, [length-width ratio (1.7 –)2.5 – 7(– 10.5)], thinly coriaceous, 0.18 – 0.24 mm thick, attenuate to obtuse (rarely retuse), acuminately mucronate at tip, narrowly to abruptly, often obliquely cuneate at base, at margins moderately to strongly crisped, irregularly, sharply serrate to partially doubly serrate with (6 –)7 – 10(– 14) teeth per 5 cm, [(1 –)2 – 3(– 4) per 1 cm], larger serrations (1 –)1.5 – 4(– 5) mm long, acute-acuminate, divergent or often inwardly hooked or curved at tips, often with sessile glands in axils of serrations and/or between serrations occasionally manifested as reduced secondary serrations 0.5 – 1.0 mm long; lamina glabrous, dark green with yellow mid and secondary veins, lustrous above, more yellow green with raised yellow midvein, glabrous, sometimes accumulating waxy deposits beneath; petioles (14 –)25 – 55 mm long, [(0.23 –)0.3 – 0.6(– 0.75) times as long as leaf blade], slender, 0.7 – 1.0(– 1.2) thick, very narrowly winged in distal 3 – 15 mm, wings with obscure glands on margins, tomentulose, glabrate, rarely puberulent on adaxial surface. Compound corymbs 2.5 – 7 cm long,

3.5 – 9.5 cm wide; lower peduncles 10 – 42 mm long; pedicels-peduncles glabrous or puberulent-floccose, glabrate, upper bracts-bracteoles 1 – 4 mm long; hypanthia 1.5 – 2.5 mm long, 2.5 – 3.5 mm wide, to 4.5 mm wide in fruit, floccose, sparsely villous to glabrate outside; sepals 1.2 – 2(– 2.5) mm long, to 1.6 – 2 mm wide, bluntly mucronate, rarely glandular along thin margins, puberulent-floccose to glabrate outside, densely villous at tip and along margins inside; petals oblong-ovate, oblong-obovate, (3.5 –)4 – 5 mm long, 2.5 – 3.4 mm wide, broadly clawed at base; filaments 2.7 – 5 mm long; anthers 0.9 – 1.0 mm long, to 1.5 mm long wet; styles 1.3 – 2 mm long. Capsules 5 – 6.2 mm long, 3.5 – 4.5(– 5) mm wide; seeds 4.4 – 4.8 mm long, 1 – 1.3 mm wide; embryos 2 – 2.5 mm long, 0.7 – 1.1 mm wide. (figs. 13, 14).

Vauquelinia corymbosa subsp. *corymbosa* is a highly variable taxon, characterized by moderately slender young stems, erect to spreading or drooping leaf blades borne on relatively long, slender petioles mostly 25 – 55 mm long (0.3 – 0.75 times as long as the leaf blades). Leaf blades are highly variable in outline, ranging from narrowly lanceolate to broadly oblong-ovate and are usually moderately to strongly crisped, coarsely serrate, occasionally partially doubly serrate, and marginal serrations may be divergent or ascending, frequently upcurved at the tip (fig. 14).

Some specimens with long, narrow leaf blades and sharp, divergent serrations [*L. Gonzalez Q. 2393* (fig. 14c), *Hess & Wilhelm 4371* (fig. 14g), *F. Brizuela 1103*, and *C.T. Mason Jr. 2621*] approach *V. corymbosa* subsp. *heterodon* except for the tendency to lack secondary serrations and their relatively short petioles (fig. 14 c,g). In leaf-blade shape, subsp. *corymbosa* approaches subsp. *karwinskyi*, but the latter taxon has distinctly shorter petioles (fig. 17). In some plants from the Cerro de Santa María near Atotonilco el Grande, northeast of Pachuca, Hidalgo, largest leaf blades are more broadly oblong-ovate to broadly ovate, (42 –)52 – 85 mm long, (14 –)20 – 43 mm wide, mostly 1.7 – 3.3(– 4.7) times longer than wide (fig. 14b) and in this broad leaf-blade characteristic differ from other populations of subsp. *corymbosa*. However, a population collection by Hess from the site (*Hess 4376*) reveals that the broad leaf-blade characteristic is not consistent throughout the population, and the population is thus not distinguished nomenclaturally.

The common name of "Palo Alto" is recorded on a specimen from Querétaro by McVaugh (*10355*). The names "Arbol prieto, Guayúl, Guayule, Palo prieto, Palo verde, Ucas" are listed for this taxon in Martinez (1979). Hess (*4376*) recorded the name "Palo Real" on a specimen from Atotonilco, Hidalgo.

Vauquelinia corymbosa subsp. *corymbosa* is restricted to limestone, xeric to

Fig. 13. Distribution of subspecies of *Vauquelinia corymbosa* and of *V. australis* in México and southwestern United States.

mesic hillsides in Matorral Xerofilo to just below the pine belt in valleys and mountains of northern Hidalgo and Querétaro (fig. 13) from 2000 to 2700 m elevation, where it occurs in association with species of *Acacia*, *Brahea*, *Helietta*, *Juniperus*, *Karwinskia*, *Leucophyllum*, *Opuntia*, *Satureja*, *Rhus*, *and Robinia*.

Representative collections: MÉXICO. **Hidalgo**: Ixmiquilpan, Aug 1905, *Rose, Painter & Rose 9159* (GH, NY, US); 12 mi S of Ixmiquilpan, 29 Oct 1966, *C.T. Mason Jr., 2621* (ARIZ); 2.5 km al ENE de Don Guiñó, Mcpio. de Alfayayucan, 4 May 1974, *F. Brizuela*

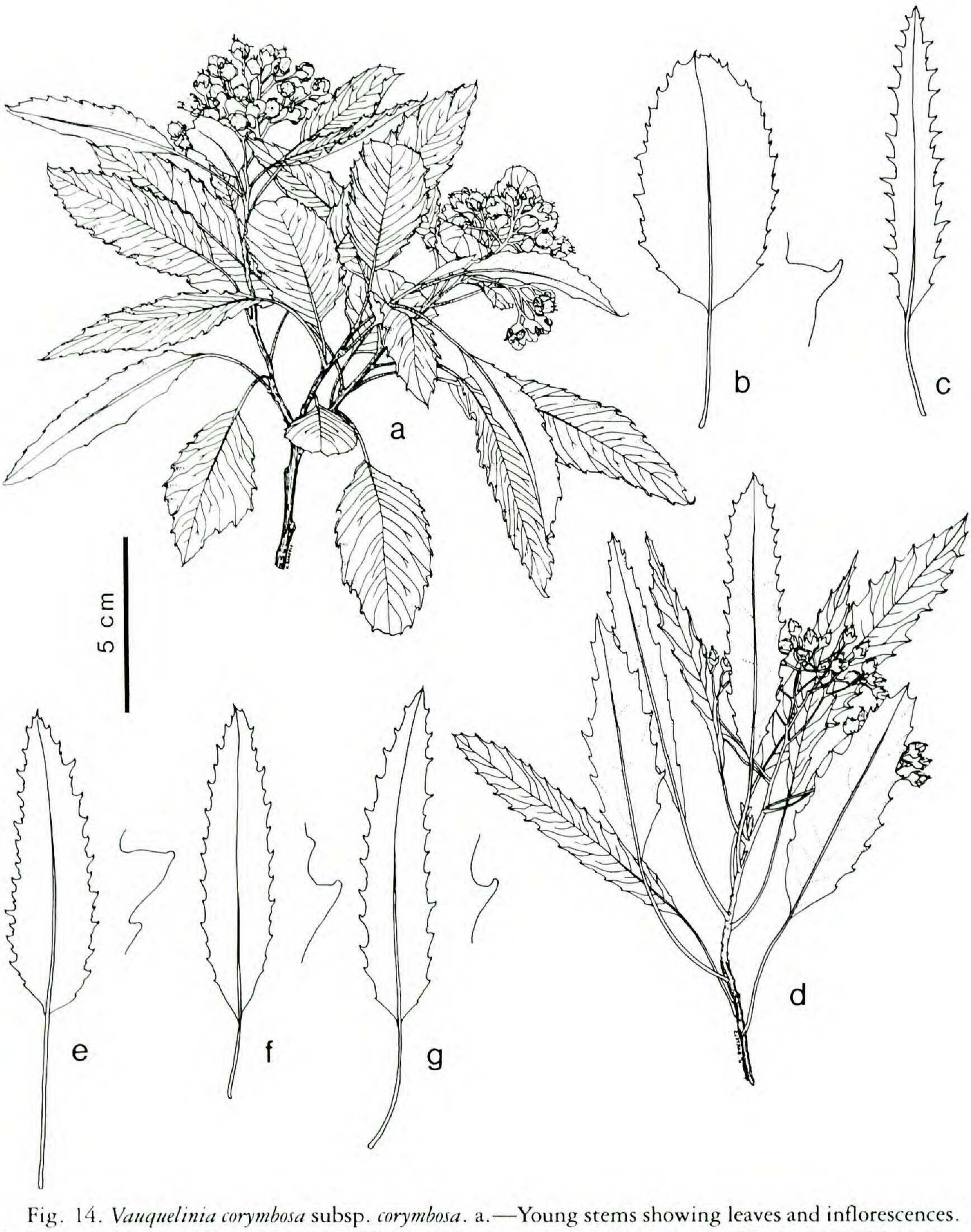


Fig. 14. *Vauquelinia corymbosa* subsp. *corymbosa*. a.—Young stems showing leaves and inflorescences. Note long petioles and variation in leaf-blade shape on specimen. From north of Pachuca, Hidalgo. *Hess & Byrne 4655*. b.—Broadly elliptical leaf from same specimen as in a. c.—Narrow leaf with some double serrations as in subsp. *heterodon*. From NNE of Actopan, Hidalgo. *L. Gonzalez Q. 2393*. d.—Young stem of plant from N of Bernal, Querétaro showing similar long petioles but narrower leaves. *Hess & Wilhelm 4371*. e-g.—Leaf outline and expanded margins from specimens from Querétaro showing variation in marginal serrations. e.—With well developed double serrations from between Pilon and Pinol de Amoles. *McVaugh 10355*. f.—With partial development of double serrations from near Bernal. *Rzedowski 25567*. g.—With single serrations from near Bernal. *Hess & Wilhelm 4371*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

1103 (CAS, MEXU); Cerro San Miguel, 14 km al NNE de Actopan, 6 May 1965, *L. González-Q. 2393* (SD 2 sheets, F, LL, MICH); NW crest of Cerro Soyutla, 6 km S of Atotonilco, 25 Sep 1976, *Clausen 76-48* (MICH, MEXU, US); Cerca de San Cristobal, Mcpio. de Cardonál, 21 Mar 1977, *Rzedowski 346734* (ARIZ, CAS, MICH); Cerro de Santa Maria, cerca de Laguna, Mcpio. de Atotonilco el Grande, 25 Nov 1973, *Rzedowski 31515* (ENCB, MEXU, MO, MICH); 5 mi N of Atotonilco, 16 Jun 1978, *Hess & Wilhelm 4376* (MOR). **Querétaro**: above Pilon on road to Pinal de Amoles, 24 Apr 1949, *McVaugh 10355* (DS, GH, LL, MEXU, MICH, MO − 2 sheets, TEX, UC); 13 mi NE of Peña Blanca, 20°40′W, 99°40′W, 5 Jun 1919, *Hess & Byrne 4644* (MOR); 3 km al NE de Bernal, sobre el camino a Toliman, 23 Mar 1968, *Rzedowski 25567* (ARIZ, DS, LL, MICH − 2 sheets), US).

3b. VAUQUELINIA CORYMBOSA subsp. **heterodon** (I.M. Johnston) Hess & Henrickson comb. et stat. nov. *Vauquelinia heterodon* I.M. Johnston. J. Arnold Arbor. 21:258. 1940. TYPE: MÉXICO. COAHUILA: road from Monclova south to Saltillo, 40 km s of Monclova, Sierra Gavia, 5 mi n of Saucillo, frequent in canyon slopes and along canyon bottom, 10 − 20 ft high, 27 − 30 Aug 1938, *I.M. Johnston 7217* (HOLOTYPE: GH!; ISOTYPE: US!).

Small trees to multi-stemmed shrubs 2 − 6(− 10) m tall; young stems initially tomentulose, soon or rarely tardily glabrate. Leaves ascending; leaf blades lanceolate, oblong-lanceolate, (5 −)7 − 14(− 17) cm long, (7 −)10 − 23(− 25)[− 30] mm wide, [leaf length-width ratio 4.3 − 7.5(− 9)], coriaceous, 0.18 − 0.3 mm thick, gradually tapering to an attenuate tip, abruptly to gradually, often obliquely cuneate at base, at margins plain or strongly crisped, coarsely, sharply doubly serrate with (6 −)8 − 19(− 21) serrations per 5 cm, [2 − 3(− 4) per 1 cm]; larger serrations divergent or ascending, acute or acuminate below a rather blunt tip, tipped with a minute, caducous gland; larger serrations 1 − 3(− 5)[− 7] mm long, secondary serrations 0.4 − 1 mm long, mostly ascending, commonly with small glands in axils of both large and small serrations; lamina glabrate, dark green with yellow mid and secondary veins, lustrous above, more yellow- or gray-green with raised yellowish midvein, usually glabrous, rarely with accumulations of wax beneath; petioles (15 −)22 − 45(− 65) mm long, [(0.17 −)0.2 − 0.35(− 0.4) times as long as leaf blade], moderately slender, 0.8 − 1.2(− 1.5) mm wide distally, yellow to yellow-maroon, glabrous to sparsely puberulent, narrowly winged in distal 1 − 3(− 4) cm, wings with small caducous glands. Compound corymbs 3 − 7(− 10) cm long, 3 − 8(− 12) cm wide; lower peduncles 12 − 35 mm long, pedicels-peduncles glabrous or puberulent-floccose, glabrate; upper bracts-bracteoles subulate, (1 −)2 − 4.5 mm long with glands along margins; hypanthia (1.5 −)2 − 2.5 mm long, to 2.5 − 3.5 mm wide, to 5.5 mm wide in fruit, glabrate outside; sepals 1.3 − 2.2(− 3.5) mm long, to 1.5 − 2.2(− 2.5) mm wide, strongly

mucronate, glandular along thin margins, floccose, glabrate outside, usually densely villous at tip and along margins inside; petals broadly oblong-ovate, (3.5 –)4 – 5.3 mm long, (2.5 –)3.2 – 4 mm wide; filaments 2.7 – 5.7 mm long; anthers 0.9 – 1.1 mm long, to 1.5 mm long wet; styles 2 – 2.4 mm long. Capsules (4.5 –)5 – 7 mm long, 4 – 6.5 mm wide; seeds 4.5 – 5.5 mm long, 1.2 – 1.6 mm wide; embryos 2.3 – 3 mm long, 0.9 – 1.3 mm wide (figs. 13, 15).

Vauquelinia corymbosa subsp. *heterodon* is characterized by its relatively long, narrowly lanceolate to oblong, sharply doubly serrate leaf blades mostly 8 – 15 cm long, 10 – 23 mm wide borne on long petioles 22 – 45(– 65) mm in length (fig. 15). Most collections from throughout its range fall readily into this pattern, with variation expressed in development and orientation of leaf serrations, the degree of crisping noted in the margins (the holotype specimen has strongly crisped leaf-blade margins), the presence or absence of sessile caducous glands on sepal margins and leaf serration axils, in mature capsule and inflorescence size and development, and persistence of vestiture. Mature stems, leaves, inflorescences, and hypanthia of most collections appear glabrate; occasional plants (*Hinton 16521*) retain some tightly coiled hairs on inflorescences, stems, and petioles.

Several specimens bordering the southeastern edge of the Bolsón de Mapimí approach *V. californica* subsp. *pauciflora* in their reduced toothing and shorter petioles. A collection by *M.C. Johnston et al. (11684*, fig. 15e) from the north side of the Sierra Paila that lies some 70 km south of recent collections of *V. californica* subsp. *pauciflora*, has moderately small leaves, 4.5 – 8.5 cm long, 10 – 17 mm wide with reduced, poorly developed marginal serrations 0.5 – 1.5 mm long and petioles only 17 – 39 mm long. Although this collection has reduced leaf serrations, it can be assigned to subsp. *heterodon*, as it has moderately long petioles and a moderate development of double serrations on some leaves. Another intermediate specimen by *Wendt et al. (10110B*, fig. 15f), 20 km to the south in the same range, has even narrower leaves, 4.5 – 8.2 cm long, 5 – 11 mm wide with reduced marginal serrations seldom over 0.5 mm long that scarcely show the characteristic double serrations of subsp. *heterodon*. The collection, however, has petioles 16 – 32 mm long and in that character again approaches subsp. *heterodon* most strongly, but shows strong intergradation towards *V. californica* subsp. *pauciflora* and is considered an intermediate between the taxa. Specimens of Purpus (*4945*, fig. 15g – h) from the Sierra Parras also exhibit some intermediacy towards *V. c.* subsp. *pauciflora*, having shorter leaf blades, less well developed double serrations, and reduced petiole lengths in some leaves. But these collections show only

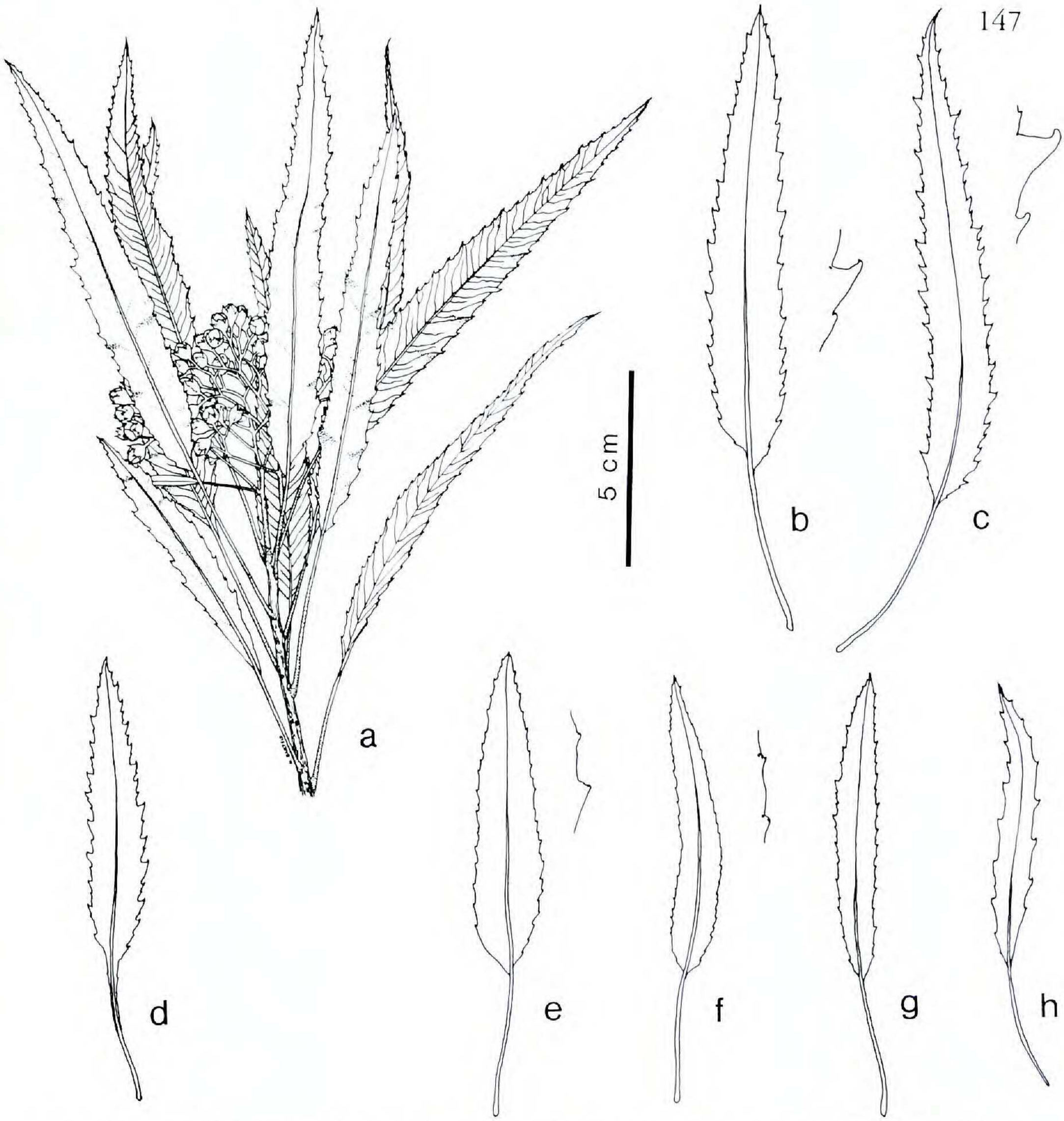


Fig. 15. *Vauquelinia corymbosa* subsp. *heterodon*. a.—Young stem with leaves and inflorescence. Near type locality in San Lazaro Pass in Sierra Gavia, Coahuila. *Hess & Wilhelm 4354*. b-h.—Leaf outlines with expanded section of margins showing variation in leaf size and marginal serrations. b.—With reduced secondary serrations from type locality. *Spetzman & Zapien 1353*. c.—With well developed double serrations from Villa de Garcia near Monterrey, Nuevo Leon. *Hernandez et al A-88*. d.—Reduced leaf from isolated population near San Carlos, Tamaulipas. *Bartlett 10207*. e-f.—Collections from Sierra Paila, NW of Saltillo, Coahuila have long petiole but fine toothing and are considered as intergrades with *V. californica* subsp. *parviflora*. e.—*Johnston, Wendt & Chiang 11684*. f.—*Wendt, Chiang & Johnston 10110B*. g-h.—Leaves from collection near Parras de la Fuente, Coahuila, showing small size, uncharacteristic single serrations. Both *Purpus 4945*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

slight convergence towards *V. c.* subsp. *pauciflora* in comparison with some collections from the northern Sierra de Paila.

Vauquelinia corymbosa subsp. *heterodon* occurs on limestone hillsides and canyons of central Coahuila from the mountains near Monclova south to the

Sierra de Paila northeast of Saltillo and in the Sierra de Parras south of Parras de la Fuente and in adjacent Nuevo León near Lampazos and the mountains northeast of Monterrey and in an isolation locality in the Sierra de San Carlos in west central Tamaulipas (fig. 13). It occurs in arid canyon scrub, oak woodland and chaparral from 650 to 2100 m elevation with a wide diversity of genera including *Acacia, Anisacanthus, Agave, Brahea, Brickellia, Bumelia, Condalia, Cordia, Dasylirion, Forestiera, Fraxinus, Gochnatia, Helietta, Jatropha, Karwinskia, Leucophyllum, Opuntia, Pistacia, Prosopis, Ptelea, Rhus, Randia, Tecoma, and Viguiera.*

The common names "Serucha" (*fide M.T. Edwards 330*, Lampazos, N.L.), "Lantrisco" (*fide Hinton 16521*, Sierra Paila), "Cercacilla" (*fide Wendt 2000*, NE Tamaulipas) have been noted for the taxon.

Representative collections: MÉXICO. **Coahuila**: Sierra de la Gloria, SE of Monclova, 3 Jul 1939, *Marsh 1923* (F, GH, TEX); Caracól Mts., 21 mi S of Monclova, Aug 1880, *Palmer 329* (AA, GH, MICH, NY, US); San Lazaro, near N entrance of El Puerto de San Lazaro, 16 Jun 1936, *Wynd & Muller 104* (ARIZ, GH, MICH, MO, NY, US); lower end of Canyon of San Lazaro, 31 mi S of Castaños, 14 Oct 1959, *M.C. Johnston 4432* (MEXU, MICH, TEX); 35 (air) mi S of Monclova, Cañón la Gavia on N side of Sierra de la Gavia, 26°21′N, 101°17′W, 2 Aug 1973, *Henrickson 11712* (TEX); Sierra Paila, Valle Seco, 1 Aug 1944, *Hinton 16521* (NY, US); Sierra de Paila, 5 mi W of Rancho La Luz, 14 Jun 1963, *Gentry, Barclay & Arguelles 20058* (US); Sierra de Paila, La Sauceda, 5 May 1967, *Marroquin 1518* (F, MEXU − 2 sheets, TEX); Sierra de la Paila, upper reaches of Cañón Corazón del Toro at Mina la Abundancia, near 25°54′N, 101°38′W, 5 Nov 1972, *Wendt, Chiang & Johnston 10110b* (LL); Mina El Aguirreno, N side of Sierra de la Paila, near 26°05′N, 101°36′W, 5 Jul 1973, *M.C. Johnston, Wendt & Chiang 11684* (LL); Parrás, Oct 1910, *Purpus 4945* (F, GH, MO, US). **Nuevo León**: Rancho Rezendez, Lampazos, 24 Jun 1937, *Edwards 330* (ARIZ, DS, F, MEXU, MO, RSA, TEX); Just E of Cerro Providencia (just SE of Candela) 26°48′N, 100°37′W, 22 Jul 1977, *Wendt 2000* (TEX); N side Sierra del Muerto, Cañón de Potrerillos, 26°01′N, 100°12′W, 16 Mar 1973, *M.C. Johnston, Wendt & Chiang 10241* (LL); 1 km adelante de Villa García, 23 Nov 1955, *Hernandez, Valdez & Miranda A-88* (MEXU); Sierra del Fraile, near Garcia Caves, 5 mi NE of Villa de Garcia, 25°53′N, 100°30′W, 17 Jun 1979, *Hess 4735* (MOR). **Tamaulipas**: Sierra de San Carlos, Cerro de los Armadillos, vicinity of San Jose, 10 Jul 1930, *Bartlett 10207* (F, GH, LL, MICH, US).

3c. Vauquelinia corymbosa subsp. **angustifolia** (Rydb.) Hess & Henrickson comb. et stat. nov. *Vauquelinia angustifolia* Rydb. N. Amer. Fl. 22:260. 1908. Type: MEXICO. Chihuahua: Santa Eulalia Mountains, 27 May 1885, *C.G. Pringle 5* (holotype: US!; isotypes: AA!, F − 2 sheets!, GH!, LL!, NY!, RSA − 2 sheets!, UC − 2 sheets).

Multi-stemmed, erect, ovoid shrubs 1.5 − 3(− 5) m tall; young stems initially tomentulose, soon or tardily glabrate with a close vestiture of crinkled hairs. Leaves ascending, erect to spreading; leaf blades linear to linear-oblong, (3.5 −)6 − 13(− 18.5) cm long, (3 −)5 − 9(− 12)[− 15] mm wide, [length-width ratio (6.5 −)16 − 24(− 37)], coriaceous,

0.2 – 0.32 mm thick, acute, obtuse, often mucronate at tip, gradually, often obliquely cuneate at base, at margins coarsely to obscurely serrate, serrulate, occasionally partially doubly serrate with (3 –)5 – 10 (– 14)[– 20] teeth per 5 cm (0 – 4 per 1 cm), serrations ascending to divergent, 0.2 – 1.5(– 2)[– 3] mm long, acute-acuminate or reduced to rounded crenulations, usually terminating with a sessile, caducous gland with persisting dark base at inside tip, often with a sessile gland in axil of serration and occasionally along margin between major serrations, these sometimes manifested as secondary serrations to 0.5 mm long, rarely entire or serrations unevenly or poorly developed; lamina initially tomentulose with hairs 0.3 – 0.5 mm long, soon or somewhat tardily glabrate, the remaining hairs to 0.1 mm long, green, yellow-green, with yellow mid and secondary veins, glabrate, lustrous above, more yellow-green with yellow, raised midvein beneath; petioles (6 –)9 – 28(– 40) mm long, [(0.07 –)0.1 – 0.2(– 0.33) times as long as leaf blade], glabrous or puberulent adaxially, wings narrow, tapering nearly to base. Compound corymbs 2.5 – 5.5 cm long, (3 –)3.5 – 6(– 7) cm wide; lower peduncles 8 – 27 mm long; pedicels-peduncles glabrate or minutely puberulent with coiled hairs; upper bracts-bracteoles subulate, 0.7 – 3 mm long; hypanthia 1.7 – 2.5 mm high, 2.5 – 3.8 mm wide, to 4.7 mm wide in fruit, initially tomentulose, glabrate or puberulent, floccose outside, glabrous above a sericeous base inside; sepals (1.3 –)1.5 – 2.4 mm long, 1.5 – 2.3 mm wide, acute, bluntly mucronate, glandular along thin margins, glabrate to floccose-villous outside, strongly tomentulose-villous inside and along margins; petals broadly oblong-ovate, ovate, 2.4 – 4.5(– 5.6) mm long, 2 – 3.5 mm wide, broadly clawed at base; filaments 2.6 – 5 mm long; anthers 0.6 – 1.1 mm long, to 1.4 mm long wet; styles 2 – 2.2 mm long. Capsules 5 – 7.5 mm long, 3.7 – 5.4 mm wide; seeds 4.3 – 6 mm long, 1.2 – 1.6 mm wide; embryos 1.6 – 2.4 mm long, 1.0 – 1.2 mm wide. Chromosome number $n = 15$ (Goldblatt 1976). (figs. 13, 16).

Vauquelinia corymbosa subsp. *angustifolia* is characterized by its uniformly narrow linear to oblong-linear leaf blades with coarse marginal serrations (fig. 16). In these features, subsp. *angustifolia* appears most similar to subsp. *heterodon* (fig. 15), but subsp. *angustifolia* has more uniformly narrow leaf blades (3 –)5 – 9(– 12) mm wide, while those of subsp. *heterodon* are more lanceolate to oblong-lanceolate, broader in the lower half, (7 –)10 – 23(– 25) mm wide, and are usually doubly, not once, serrate. The petioles of subsp. *heterodon* also tend to be much longer, (15 –)22 – 45(– 65) mm long versus (6 –)9 – 28(– 40) for subsp. *angustifolia*. *Vauquelinia corymbosa* subsp. *heterodon* also tends to form distinct trees while subsp. *angustifolia* is usually a multi-stemmed shrub.

Throughout its range, subsp. *angustifolia* exhibits considerable diversity in leaf blade size and shape. Plants from the western portions of its range, including those from the type locality, tend to have much broader leaf blades, 8.5 – 12 mm wide (including serrations), with leaf-blade length-width ratios ranging from 6.5 to 12 (fig. 16f – g). In contrast, plants from Texas and southward tend to have narrower leaf blades (3 –)5 – 9, only rarely to 12 mm wide, with leaf blade length-width ratios of (7 –)16 – 24(– 37), with the smallest ratios originating from very narrow, short leaves (fig. 16 b – d). Some of these plants also tend to have more distinctly glabrate inflorescences. Analyses by Hess, however, show no statistically significant differences between these populations.

Occasional plants of very arid exposed habitats have shorter, narrower leaf blades measuring 5 – 9 cm long, 3.5 – 6.5 mm wide, with marginal serrations only 3 – 5 mm apart [*I.M. Johnston & Muller 549*, (fig. 16j)]; others have much longer leaves to 21 cm in total length (including a petiole 2.5 cm long) with serrations up to 17 – 20 mm apart [*I.M. Johnston 9313*, (fig. 16b)]. Generally the number of serrations, measured as the number per 5 cm of margin, is greatest in small leaves with some doubled serrations.

One specimen from the Sierra de los Pinos of northern Chihuahua [*LeSueur 1531*, (fig. 16e)] has very narrow leaf blades, with some leaf blades weakly serrulate and others entire. The entire leaf blades range from 5 to 13 cm in length, 3 – 5 mm in width, with the longest leaves lacking serrations altogether. As in other taxa of the genus, leaf-blade toothing varies considerably. Most specimens have one series of divergent or ascending, acute-acuminate serrations that measure from 0.5 – 1.5 mm long. In some plants, serrations are more pronounced, measuring to 3 mm in length as in *Chiang et al. 8387* (LL), but this is rare. In others, they are reduced to small, rounded, gland-tipped knobs under 0.5 mm long, as in *M.C. Johnston et al. 11310* (fig. 16i). Occasional plants show partial development of secondary serrations, making some leaf blades partially doubly serrate.

Minor variation is also known in flower characteristics, particularly in petal size and shape, with some plants tending to have narrow, more oblong-ovate petals.

Vauquelinia corymbosa subsp. *angustifolia* occurs mostly on limestone, rarely igneous-rock slopes and canyons, and also on gypsum flats from eastern Chihuahua, southern trans-Pecos Texas south to central Coahuila

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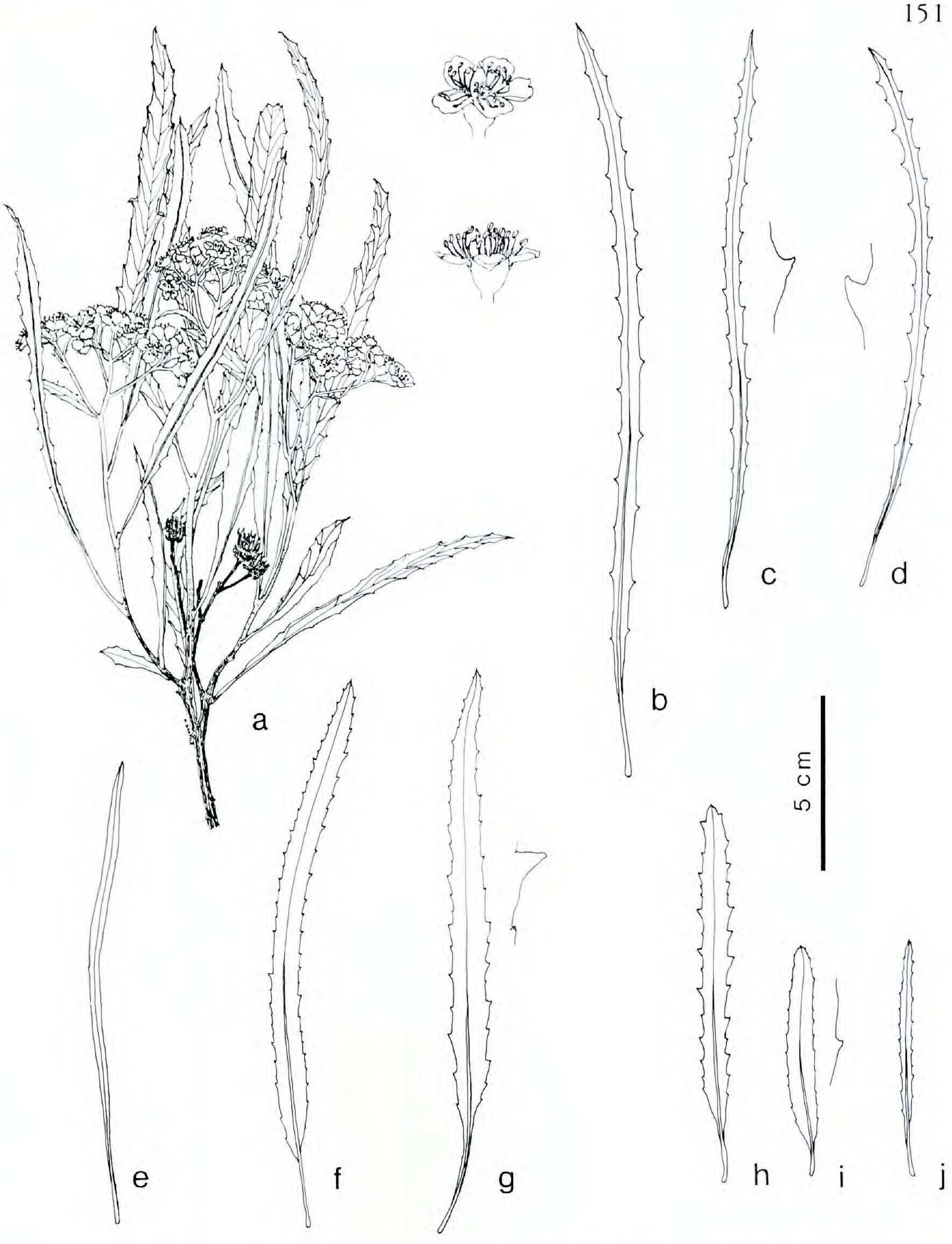
Fig. 16. *Vauquelinia corymbosa* subsp. *angustifolia*. a.—Young stem showing narrow leaves and inflorescences. Inserts show flowers. b-j.—Outline drawings of leaves, some with marginal toothing shown expanded, showing variation in shape, size, and petiole length. b.—Typical but very long leaf from Sierra de la Madera, Coahuila. *I.M. Johnston 9313*. c.—Typical narrow leaf from Chisos



Mountains, Texas. *Lundell & Lundell 14606*. d.—Typical leaf from Sierra de Zacatosa, W of Cuatro Ciénegas, Coahuila. *Chiang et al 12100A*. e—Aberrant, entire, very narrow leaf from collection of Sierra de los Pinos in NE Chihuahua. *LeSueur 1531*. f-g.—Collections from western portion of range often have broader laminas. f.—From Santa Eulalia Mountains near Cd. Chihuahua, Chihuahua (type locality). *Pringle 369*. g.—Similar broad leaf from Sierra Morrión in NE Chihuahua. *Chiang, Wendt & Johnston 8387*. h.—Atypical short, broad leaf from collection from SW flank of Sierra del Carmen in N Coahuila. *Chiang, Wendt and Johnston 9271*. i.—Abnormal very short leaf from Sierra de Parra in NE Chihuahua. *Johnston, Wendt & Chiang 11310*. j.—Very reduced, narrow leaf from Sierra Santa Fe del Pino in N Coahuila. *I.M. Johnston & C.H. Muller 549*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

(fig. 13), from 1050 to 1500 m elevation, where it occurs in the Chihuahuan Desert canyon scrub and chaparral with genera and species such as *Acacia berlandieri, A. rigidula, Bouvardia, Buddleja, Cercocarpus montanus, Chilopsis linearis, Diospyros texana, Eysenhardtia, Fallugia paradoxa, Fraxinus greggii, Gutierrezia, Juglans, Juniperus, Mimosa, Pinus cembroides, Quercus, Rhus virens, Ungnadia, Viguiera* and *Yucca*.

R.M. Stewart (962, GH) reports the common name of "Barreta" on a collection from northern Coahuila.

Representative collections: U.S.A.: TEXAS. **Brewster Co.**: Chisos Mts., ridge on E side of Juniper Cañón, 15 – 18 Jul 1921, *Ferris & Duncan 2927* (CAS, DS, NY); Chisos Mts., Blue Creek Canyon, 23 Jun 1931, *Moore & Steyermark 3203* (AA, CAS, DS, MICH, NY, UC); Chisos Mts., Oak Creek Canyon near Camp and the Window, 5 Jul 1937, *Sperry 168* (US); Mid-slopes of Dead Horse Mountains, near Sue Peak, Big Bend Nat. Park, 19 Jul 1952, *Warnock 10778* (LL). **Presidio Co.**: Chinate Mts., 11 Sep 1914, *Young s.n.* (TEX).

MÉXICO: **Chihuahua**. Sierra de Pinos, Dec 1937, *LeSueur 1531* (ARIZ, F, GH, TEX); Sierra de la Parra, across river from Sierra Vieja, 30°00′N, 104°52′W, 13 Jun 1973, *M.C. Johnston, Wendt & Chiang 11310* (LL); Ca 27 mi NE of El Morrión, ca 9 mi NE of RR crossing near Hwy 16, 13 Jul 1972, *A.M. Powell 244* (TEX); 21 km SW of Coyame on SE flank of Sierra de la Escondida, 29°22′N, 105°15′W, 22 Oct 1972, *Wendt, Chiang & Johnston 9814* (MO, LL); S and SE of Mina la Nueva Esperanza, E slope of Sierra del Morrión, 28°55′N, 105°21′W, 10 Jul 1972, *Chiang, Wendt & Johnston 8387* (LL); Santa Eulalia Mountains, 14 Aug 1885, *Pringle 369* (AA, F, GH, LL, MO – 2 sheets, NY – 2 sheets, US – 2 sheets); NW end of Sierra del Diablo, 29 – 30 Jul 1941, *Stewart 962* (F, LL, UC). **Coahuila**: SW flank of Sierra del Carmen, 29°04′N, 102°45′W, 15 Sep 1972, *Chiang, Wendt & Johnston 9278* (MO, LL); W Slope of Sierra del Jardín above (E of) Rancho El Caballo, 29°03′N, 102°38′W, 16 Sep 1972, *Chiang, Wendt & Johnston 9322* (LL); head of Cañón Ybarra, Sierra del Pino, 29 Aug 1941, *Stewart 1255* (F, GH, LL); Sierra del Pino, N of great cliffs about 10 mi N of Camp at La Noria, 22 Aug 1940, *I.M. Johnston & Muller 549* (GH, MICH, TEX); Crest of Sierra Planchada, N of Esmaralda, 25 Sep 1941, *I.M. Johnston 9392* (GH); Puerto de la Arena, Sierra Zacatosa, 7 km W of Zacatosa, 27°02′N, 102°48′W, 7 Aug 1973, *Chiang et al. 12100A* (LL); 2 km SW of Puertecito, W end of Sierra de la Madera, 21 Sep 1941, *I.M. Johnston 9313* (GH, LL); S part of Sierra de los Organos, 26°43′N, 103°01′W, 8 Aug 1973, *M.C. Johnston et al. 12125* (LL).

3d. VAUQUELINIA CORYMBOSA subsp. **karwinskyi** (Maxim.) Hess & Henrickson comb. et stat. nov. *Vauquelinia karwinskyi* Maxim. Trudy Imp. S.-Peterburgsk. Bot. Sada (Acta Horti. Petrop.) 6:236. 1879. TYPE: MÉXICO. TAMAULIPAS: Santyaguillo (Santiaguillo), Jun 1843, *Karwinsky 213* [LECTOTYPE: indicated by Standley (1922) as from Santiaguillo, here designated as specimen in upper left-hand corner of sheet as seen on photo at MOR! and TEX! from LE].

Vauquelinia potosina Painter ex Standl. Proc. Biol. Soc. Wash. 31:131. 1918. TYPE: MÉXICO. LUIS POTOSÍ Alvarez, 19 – 22 May 1905, *E. Palmer 594* (HOLOTYPE: US!; ISOTYPES: F! LL! MO – 2 sheets!).

Erect small trees with rounded to ovoid crowns to multi-stemmed shrubs 2 – 6(– 8) m tall; young stems initially tomentulose with crinkled hairs,

soon or occasionally tardily glabrate and puberulent. Leaves erect-ascending; leaf blades oblong-lanceolate, oblong-elliptical, oblong, oblong-ovate to ovate, rarely linear, (3−)4−9(−13.2) cm long, [5.5−]10−25(−36) mm wide, [length-width ratio (1.8−)2.2−5(−7)[−14]], coriaceous to stiffly coriaceous, 0.26−3.5 mm thick, acute, obtuse to rounded, usually mucronate at tip, abruptly to gradually, obliquely cuneate to rounded at base, at margins weakly to strongly crisped, uniformly, occasionally coarsely serrate to partially doubly serrate with (7−)10−14(−17) serrations per 5 cm [(1−)2−3 per 1 cm], serrations ascending or divergent, acute-acuminate or reduced to low rounded crenulations, (0.2−)0.5−2.5(−5.5) mm long, sometimes barely expressed; lamina flat or slightly conduplicately rounded, green to yellow-green, glabrous with yellow midveins above, yellow-green, glabrous, rarely with accumulations of wax, with rounded, raised, yellowish or slightly reddish midvein beneath; petioles (5−)7−27(−34) mm long, [(0.09−)0.15−0.3(−0.4) times as long as leaf blades], 0.9−1.5 mm thick, narrowly winged in distal half, often with sessile glands along wings, usually reddish to maroon brown, glabrous or puberulent adaxially. Compound corymbs 2−6.5(−8) cm long, (3−)5−10.5 cm wide; lower peduncles 15−40 mm long; pedicels-peduncles glabrate or tardily glabrate and puberulent-floccose; upper bracts-bracteoles subulate, 1−4.5 mm long with glands on margins; hypanthia 1.5−2.0(−2.5) mm long, 2.2−3.0 mm wide to 4.5 mm wide in fruit, glabrate to tardily pubescent-floccose outside, glabrous inside except at base; sepals (1.2−)1.5−2.0 mm long, 1.5−2.0 mm wide, bluntly mucronate, glandular along margins, glabrate or variously tardily floccose outside, mostly villous to sericeous inside and along margins; petals broadly oblong-ovate, ovate, 3−4(−4.5) mm long, 1.8−3 mm wide, broadly clawed at base; filaments 2.7−4.5(−5.2) mm long; anthers 0.7−1 mm long, to 1.2 mm long wet; styles 1.6−2.2 mm long. Capsules 4.5−6 mm long, 3−4.5 mm wide; seeds 3.5−5 mm long, 1−1.2 mm wide; embryos 1.7−2.3 mm long, 0.7−1.2 mm wide. (figs. 13, 17).

Vauquelinia corymbosa subsp. *karwinskyi* is characterized by its generally oblong, oblong-lanceolate, oblong-ovate, oblong-elliptical, usually relatively thickened, erect, serrate, partially doubly serrated leaf blades borne on moderately short, thickened, often reddish petioles (fig. 17).

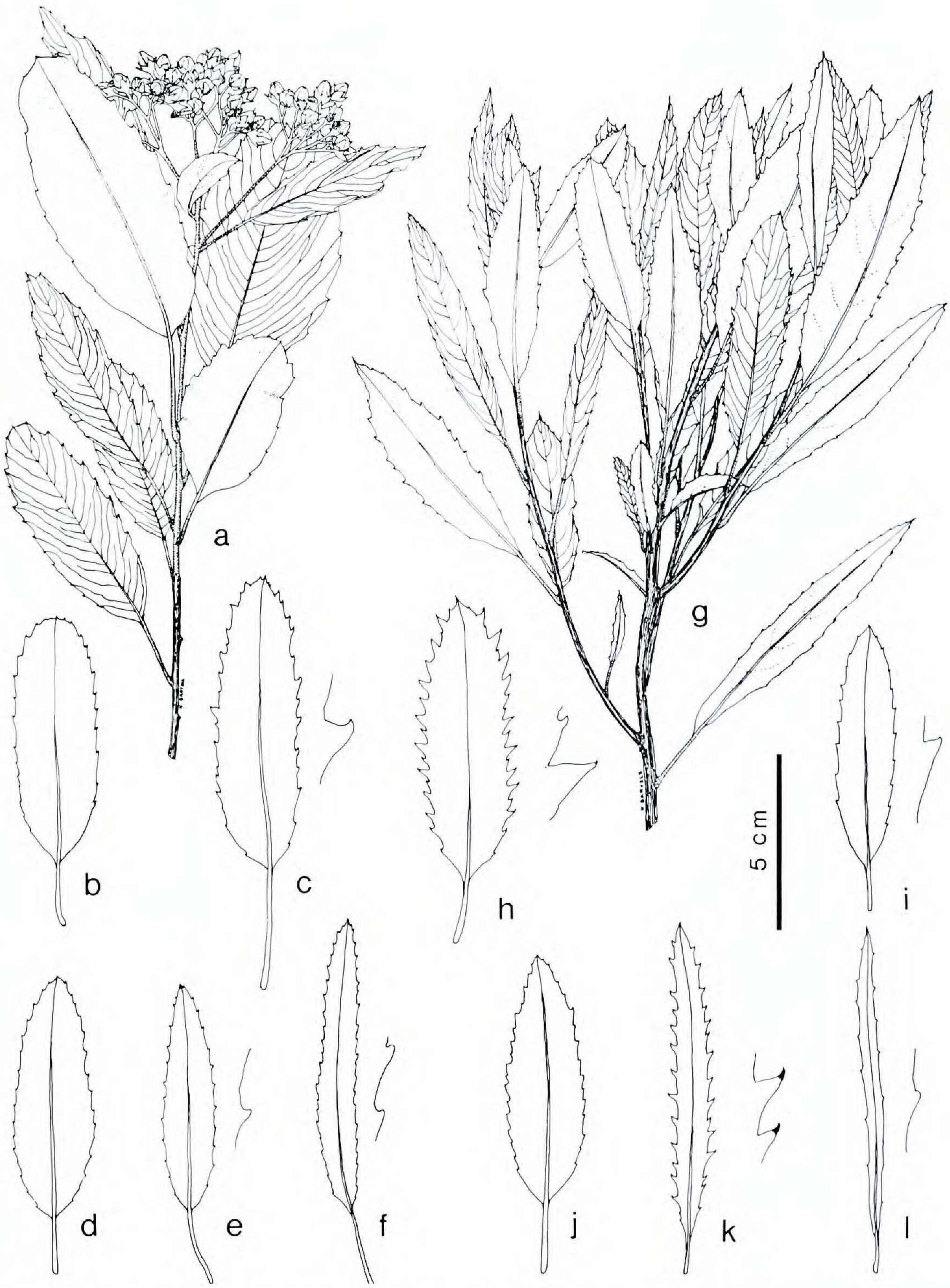
It differs from subsp. *corymbosa* by its much shorter, thicker petioles and more oblong, usually thicker leaf blades, from subsp. *heterodon* by its shorter leaf blades and petioles and by its much less pronounced serrations, from subsp. *saltilloensis* by its longer leaf blades and its tendency to have more glabrate inflorescences and stems, and from subsp. *latifolia*, with

which it is sometimes sympatric, by its narrower, non-glaucous leaf blades and its bushier, broader growth habit.

Vauquelinia corymbosa subsp. *karwinskyi* occurs along the western margin of the Sierra Madre Oriental with collections known from the state of San Luis Potosí east and northeast of Ciudad San Luis Potosí near San Francisco-Alvarez and near Guadalcazar and in Tamaulipas in the area around Miquihuana and Bustamente (fig. 13). In 1918, Standley named the San Luis Potosí populations *Vauquelinia potosina*, distinguishing them from those of the Tamaulipan *V. karwinskyi* on the basis of leaf morphology noting that the latter had broader leaves with more obtuse to truncate leaf bases. However, he later combined the two taxa in his *Trees and Shrubs of México* (Standley 1922). Some differences do exist between the San Luis Potosí and Tamaulipas populations. Those in San Luis Potosí tend to be taller trees with rounded crowns and single trunks and also tend to have slightly thinner leaf blades with more pronounced serrations and longer petioles, (11−)14−24(−31) mm long. In contrast, plants from Tamaulipas generally occur in more arid habitats, have a more ovoid, branched shrub to small tree habit, and tend to have thicker, more yellowish, somewhat conduplicately rounded leaf blades, with less pronounced marginal serrations and thicker, shorter petioles, (6−)9−17(−22) mm long. The leaf base and tip differences noted by Standley (1918) for erection of *V. potosina* are not consistent, as shown in representatives from a population collection by Hess & Byrne (*4642*, fig. 17b−f). It would be very difficult to define reliable differences between these population systems except for geography, as both populations are so variable in their leaf characteristics.

Occasional plants in Tamaulipas populations have much narrower leaf blades. A collection by González-Medrano *et al.* (*8672*) has linear leaf blades to 13 cm long and 5.5 mm wide, and in these characters is completely referable to *V. c.* subsp. *angustifolia*. Our collections from this region revealed an additional narrow-leaved collection (*Henrickson & Hess 19236*, fig. 17l) and an adjacent series of intermediate collections with broader, oblong-lanceolate, strongly serrate leaves (*Henrickson & Hess*

Fig. 17. *Vauquelinia corymbosa* subsp. *karwinskyi*. a-f.—Variation in leaf structure from collections from mountains E of Cd. San Luis Potosí. a.—Young stem showing leaves and inflorescence. Note variation in leaves. From collection 35 mi E of Cd. San Luis Potosí. *Hess & Byrne 4642*. b-f.—Leaf outlines showing variation in leaf shape, serrations, and petiole length from a population collection 20 mi E of Cd. San Luis Potosí. *Hess & Byrne 4631*. g-l.—Variation in leaf structure from collections from vicinity of Miquihuana, Tamaulipas. g.—Young stem showing narrow, erect-ascending, relatively thickened leaves. *Hess & Wilhelm 4357*. h-l.—leaf outlines showing extreme variation in leaf shape, serrations and petiole length from various collections. h-i.—Variation of one population in leaf shape and serration. *Henrickson & Hess 19094*. j.—Leaf outline from *Johnston, Chiang & Wendt 11176*. k-l.—A



local stand ca 10 km NW of Miquihuana has large individuals with abnormally narrow leaves. k.—*Henrickson & Hess 19240*. l.—This plant has leaves referable to *V. c.* subsp. *angustifolia*, but habit of plant and other features cause it to be referred to this taxon. *Henrickson & Hess 19236*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

19238, 19240, fig. 17k; see also *González-Medrano et al. 8672*) that approaches subsp. *heterodon* in leaf outline and serrations, though it lacks the long petiole characteristic of that taxon. Whether these narrow-leaved individuals represent true subsp. *angustifolia* brought in by long-distance dispersal or isolated here in post-pluvial times, or merely represent autochthonous extremes in variations of subsp. *karwinskyi* can only be resolved by further studies. As the leaves approach the texture of subsp. *karwinskyi* and the inflorescence and hypanthium are quite glabrous and lustrous, we here include these plants within the range of variation of subsp. *karwinskyi* until further evidence is obtained. Clearly the subsp. *heterodon*-like individuals with their shorter petioles and lack of consistent secondary serrations need not be referred to subsp. *heterodon*.

Vauquelinia corymbosa subsp. *karwinskyi* occurs in semi-arid limestone slopes from 1600 to 2300 m in association with species as *Juniperus flaccida, Pinus pinceana, P. nelsoni, Quercus pringlei, Q. rugosa, Rhus virens, Cornus excelsa, Prunus tetradenia, Juglans mollis, Helietta parvifolia, Forestiera reticulata, Yucca filifera, Agave lecheguilla* and species of *Dodonaea, Comarostaphylis, Cercocarpus, Lindleya, Cowania, Gochnatia, Garrya, Krameria, Dasylirion*, and *Nolina*.

Representative collections: MÉXICO. **San Luis Potosí**: 20 mi S of Huizache Jct. on Mex 54, 3 mi E on road to Guadalcazar, 22°42′N, 100°47′W, 14 Jun 1979, *Hess & Byrne 4705* (MOR); Cerro de San Cayetano, Guadalcazar, 23 Oct 1891, *P. Maury 7489* (NY[6]2 sheets); 20 mi E of San Luis Potosí on Mex 70, 22°04′N, 100°41′W, 5 Jun 1979, *Hess & Byrne 4631* (MOR); 35 mi E of San Luis Potosí, 8 mi E of San Francisco on Mex 70, 22°03′N, 100°32′W, 5 Jun 1979, *Hess & Byrne 4642* (MOR); Minas San Rafael, Jun 1911, *Purpus 5207* (F, GH, MEXU, MO, NY, UC, US). *Tamaulipas*: 12 km al N de La Perdida, Sierra de las Mulas, 20 Apr 1976, *González-Medrano et al. 8795* (MEXU); 15 km N de la Perdida, rumbo a Valle Hermoso, 16 Apr 1976, *González-Medrano et al. 8672* (CAS, MEXU, MO); 10 km NW of Miquihuana, along lower road to Marcela, 23°37′N, 99°52′W, 9 Oct 1982, *Henrickson & Hess 19238* (MOR, RSA); same area, date, *Henrickson & Hess 19240* (MOR, RSA); same area, date, *Henrickson & Hess 19236* (MOR, RSA); near town of Miquihuana, 23°42′N, 99°45′W, 8 Aug 1941, *Stanford, Retherford & Northcraft 780* (ARIZ, DS, GH, MO, NY, UC); 8 km by winding road N of Bustamente towards Miquihuana, 23°23′N, 99°51′W, 21 May 1973, *M.C. Johnston, Wendt & Chiang 11176* (LL); 14 km al SE de Palmillas, al W of Rancho "El Balcon", 24 Aug 1976, *González-Medrano, Sandoval C. & Zavaleta B. 9987* (MEXU, MICH).

3e. Vauquelinia corymbosa subsp. **saltilloensis** Hess & Henrickson subsp. nov.

A *Vauquelinia corymbosa* subsp. *karwinskyi* distincta laminis brevioribus pro parte (2.4−)3−5(-raro 7) cm longis [non (3−)5−9(−13.2) cm longis] et petiolis brevioribus (4−)5−11(−14) mm longis [non (6−)9−17(−34) mm longis] et caule et inflorescentiae vestimento persistioribus, et statura abbreviore.

Multi-stemmed shrubs to small trees 1−2.5(−4) m tall; young stems

moderately villous-canescent, persistently puberulent with short coiled hairs. Leaves erect-ascending, occasionally spreading; leaf blades variable in outline, ovate, elliptical to narrowly or broadly or oblong-ovate, or oblong-elliptical, (2.4−)3−6(−7) cm long, (10−)12−24(−33) mm wide, [length-width ratio (1.3−)1.7−3.2(−4.5)], coriaceous, 0.2−0.31 mm thick, acute to obtuse, occasionally irregularly retuse, mostly mucronate at tip, narrowly to broadly, often obliquely cuneate, more subrounded when broad at base, at margins plain or variously crisped, serrate, doubly serrate or partially doubly serrate with 2−5(−8) serrations per 1 cm, teeth ascending to divergent, 0.2−1.6 mm long, slender, acute-acuminate or low and blunt with sessile glands on inside margin at tip, often with sessile glands in axils of serrations and along margins between major serrations, these sometimes manifested as reduced secondary, slender, acuminate or blunt serrations; lamina green, lustrous, glabrate but usually persistently puberulent along yellow midvein above, yellow-green and similarly puberulent along raised, yellowish midveins beneath, occasionally glabrate throughout; petioles (4−)5−11(−14) mm long, [(0.1−)0.14−0.26(−0.3) times as long as leaf blades], moderately thick, 0.7−2 mm wide, winged by tapering leaf margins nearly to base, with sessile caducous glands along wings, usually persistly puberulent with slender, curled hairs to 0.1 mm long, at least on adaxial surface or throughout. Compound corymbs 2−4.5 cm long, 2.5−7 cm wide; basal peduncles 15−30 mm long; pedicels-peduncles initially tomentulose-villous with crisped hairs to 0.1−0.2 mm long, vestiture tending to persist as a close canescence into fruiting; upper bracts-bracteoles subulate, 1.2−2(−5) mm long, with sessile marginal glands; hypanthia 1.5−2 mm long, 1.7−2.5 mm wide, to 4 mm wide in fruit, sparsely puberulent outside, glabrous inside; sepals 1.3−1.5 mm long, 1.5−2 mm wide, thick, strongly mucronate, glandular along thin margins, puberulent to subglabrate outside, villous inside at tip and margins; petals oblong-ovate, oblong-obovate, 3.5−5 mm long, 2−3.2 mm wide, tapering to a broad claw at base; filaments 2.4−4.5 mm long; anthers 0.7−1 mm long; styles 1.3−2 mm long. Capsules 4−5 mm long, 3−4.3 mm wide; seeds 3.4−4.5 mm long, 1−1.2 mm wide; embryo 1.7−2.5 mm 0.7−0.9 mm wide.

TYPE: MÉXICO. COAHUILA: Cañón de San Lorenzo, 5−6 mi SE of Saltillo, lower cañón on dry rocky mountain sides, treelike, 4 m tall, flowers white, 28 May 1951, *R. McVaugh 12345* (HOLOTYPE: MICH!; ISOTYPE: US!). (figs. 13, 18).

Vauquelinia corymbosa subsp. *saltilloensis* is characterized by its variably narrowly to broadly ovate-elliptical, short-petiolate, often unevenly, coarsely doubly serrate, relatively short leaf blades and its tendency to have

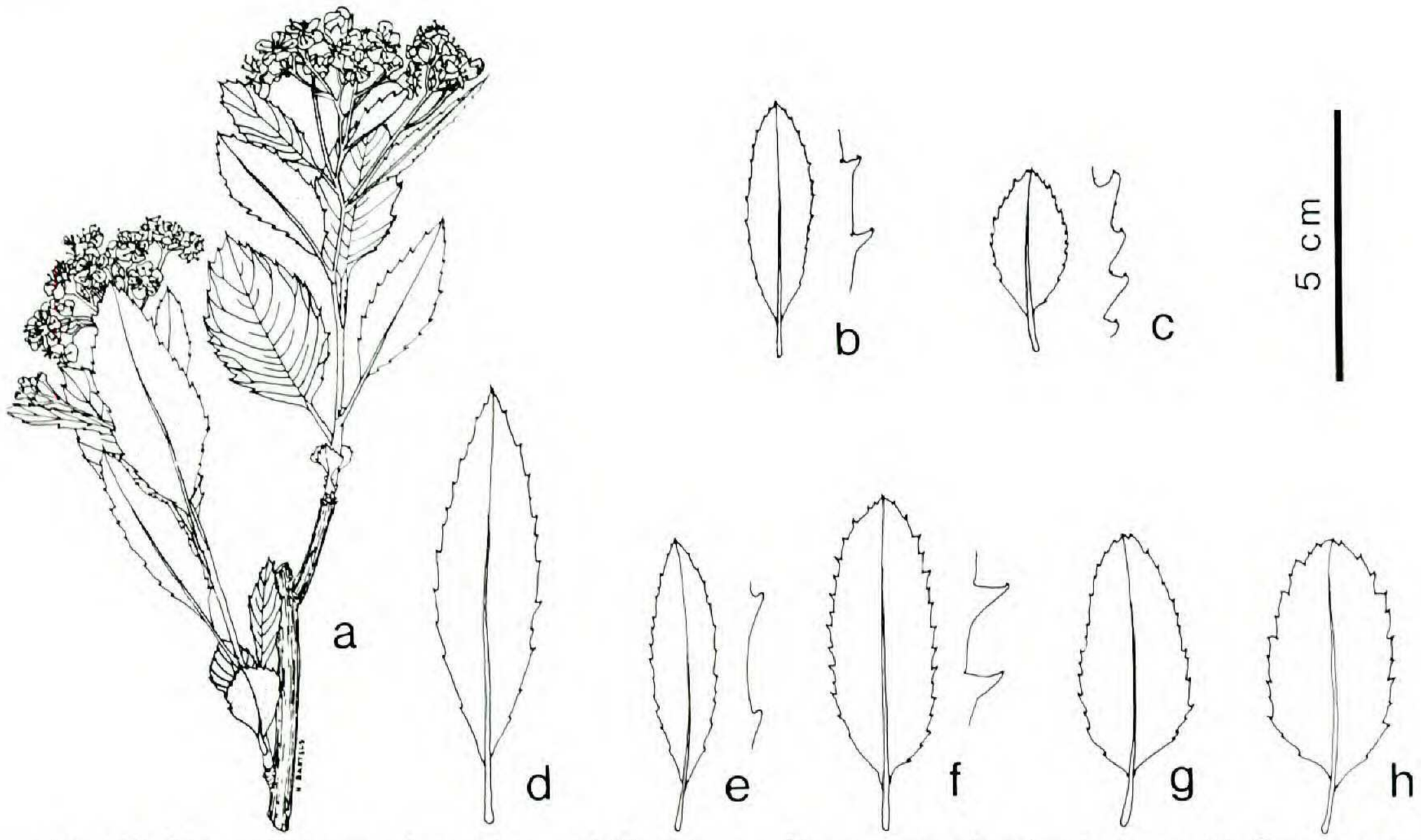


Fig. 18. *Vauquelinia corymbosa* subsp. *saltilloensis*. a.—Young stem showing leaves and inflorescence. Holotype from San Lorenzo Canyon, 5-6 mi SE of Saltillo, Coahuila. b-h.—Variation of leaf outline, serration, petioles, b.—From Saltillo area, *Hinton 18900*. c.—From near Galeana, Nuevo León. *Henrickson 18900*. e-h.—Variation in gathering from type locality in San Lorenzo Canyon, showing variation in outline and serration. *Hess & Wilhelm 4337*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

persistent hairs on the inflorescences, stems, petioles and along midveins on leaf blades and on the distinctly winged petioles (fig. 18).

The taxon is highly variable in leaf-blade shape, with some collections from the type locality having narrow- to oblong-ovate to nearly lanceolate leaf blades while other specimens have broadly oblong-ovate leaf blades (fig. 18d – h). Leaf margins are also variable, ranging from those uniformly once serrate with 5 – 8, slender, divergent serrations per 1 cm, as in *G.B. Hinton 16693* (US), to a more common type that is irregularly, often coarsely, doubly serrate with only 2 – 5 teeth per 1 cm (*Palmer 538, Henrickson 18900, Hess & Wilhelm 4337*, fig. 18b – h). As in other taxa serrations vary from prominent to very reduced, but they more often tend to be narrow.

In its coarse double serrations subsp. *saltilloensis* approaches subsp. *heterodon*, but subsp. *saltilloensis* has much shorter, broader leaf blades and shorter petioles and also tends to be more persistently pubescent on inflorescence, stems, petioles and midveins. Some specimens approach subsp. *corymbosa* in leaf shape, but they again have shorter, thicker petioles unlike that taxon. The new taxon is perhaps most similar to subsp. *karwinskyi*, which is also variable in leaf-blade shape and has similar short petioles, but subsp. *saltilloensis* has smaller leaves that more often tend to

be doubly serrate, and it is again more persistently pubescent. In its shorter petioles, the new taxon is more similar to the Tamaulipan populations of subsp. *karwinskyi* than to the San Luis Potosí specimens. Although the new taxon is highly variable, it is recognized as a distinct taxon mainly as it cannot easily be combined with any other taxon.

The new taxon occurs in mid-elevational hillsides from 1900 to 2200 m in southeastern Coahuila, with most collections from the limestone Cañón de San Lorenzo near Saltillo and from adjacent Nuevo León both from near Monterrey and near Galeana (fig. 13). It occurs in association with *Malacomeles, Acacia, Agave scabra, Baccharis, Berberis trifoliolata, Bouvardia, Comarostaphylis, Cercis, Cercocarpus, Dalea, Dasylirion, Fraxinus, Garrya, Juniperus flaccida, Lindleya, Nolina, Ptelea, Quercus, Rhus*, and *Salvia*, with an understory of *Stipa tenuissima*, and other species.

Additional collections: MÉXICO. **Coahuila**: San Lorenzo Canyon, 6 mi SE of Saltillo, 16 Apr 1905, *Palmer 538* (NY, US); Cañón de San Lorenzo, W-drainage canyon in Sierra de Pame, 5 mi due S of Saltillo, 25°20′N, 100°59′W, 23 Jul 1977, *Wendt & Valdez R. 2010* (TEX); near Saltillo, limestone hillside, 25 May 1947, *Hinton 16693* (US); 5 mi SE of Saltillo, ca 3 mi E of Mex Hwy 54, in Sierra de Poliname, 11 Jun 1978, *Hess & Wilhelm 4337* (MOR); ca 35 km E of Saltillo, road to La Carbonera, 15 – 20 km E of Hwy 57, 15 Aug 1974, *Spjut, Barclay & Sallee 4302* (CAS). **Nuevo León**: Sierra Madre Mts., Monterrey, 29 Jul 1933, *C.H. & M.T. Muller 541* (F, GH, MEXU, TEX); 5 km NNE of Galeana, 25 Apr 1982, *Henrickson 18900* (MOR).

3f. VAUQUELINIA CORYMBOSA subsp. **latifolia** (Rydb. ex Standl.) Hess & Henrickson comb. et stat. nov. *Vauquelinia latifolia* Rydb. ex Standl. Contr. U.S. Natl. Herb. 23(2):323. 1922. TYPE: MÉXICO. TAMAULIPAS: Mountains near Miquihuana, shrub 4 – 8 ft, white fl., 10 Jun 1898, *E.W. Nelson 4481* (HOLOTYPE: US!; ISOTYPES: F!, GH!, NY!).

Multi-stemmed, often slender, spindly, erect shrubs (1 –)2 – 4(– 5) m tall; young stems glabrate-glabrous, dark reddish, glaucous, thick, to 2 – 4(– 5) mm in diameter. Leaves erect-ascending, occasionally spreading; leaf blades variable in outline, ovate-lanceolate, ovate, oblong to oblong-ovate, broadly ovate, rarely nearly orbicular, (3 –)5 – 8(– 12.5) cm long, (15 –)25 – 45(– 65) mm wide, [length-width ratio (1.1 –)1.4 – 2.7(– 3.4)], stiffly coriaceous, 0.27 – 0.43 mm thick, acute, obtuse, to nearly rounded, occasionally retuse, usually distinctly mucronate at tips, broadly, obliquely cuneate, truncate, rounded or, when very broad, subcordate at base, at margins strongly to weakly crisped, often coarsely, sharply serrate or partially doubly serrate with 8 – 14(– 24) serrations per 5 cm [(1 –)2 – 5 per 1 cm], serrations ascending to divergent, acute-acuminate, apiculate, (0.8 –)1.2 – 4.5(– 6.5) mm long, rarely margins partially or completely entire, serrations only rarely with sessile glands in axils or at tip; lamina flat or variously conduplicate,

yellow-green, glabrous, glaucous with midvein yellow to dull red above, more yellow green, bluish-glaucous with midvein raised, yellowish to dull red beneath; petioles (7−)10−18(−21) mm long [0.14−0.22(−0.28)[−0.37] times as long as leaf-blade], thick, 1.2−2.5 mm in diameter, neither winged nor glandular along margins, glabrous, glaucous, dull reddish. Compound corymbs 5−10 cm long and wide; lower peduncles 12−55 mm long; pedicels-peduncles glabrate to glabrous; upper bracts-bracteoles subulate, 1−5.5 mm long, without glands on margins; hypanthia 1.5−2.5 mm long, 2.5−3 mm wide, to 5.5 mm wide in fruit, glabrous outside, glabrous inside but sericeous near ovary at base; sepals 1.5−2 mm long, 1.4−2 mm wide, thick, bluntly mucronate at tip, glabrous to floccose outside, glabrous or nearly so or slightly sericeous in mid-portion or marginally villous inside, marginal glands lacking; petals oblong-ovate, 3.5−4.5 mm long, 2−3.3 mm wide, broadly clawed at base; filaments 2.7−4.5 mm long; anthers 0.7−1.0 mm long, to 1.2 mm long wet; styles 1.7−2 mm long. Capsules 4.5−7 mm long, 4−5.5 mm wide; mature seeds and embryos not seen (figs. 13, 19).

Vauquelinia corymbosa subsp. *latifolia* is one of the more distinctive subspecies of *V. corymbosa*, distinguished by its erect, slender, often rather sparse, sucker-shoot-like growth habit with relatively thickened, erect, long-shoot stems 2−4(−5) mm in diameter. Leaves are thick, stiffly coriaceous, glabrous, glaucous, usually large, ovate, broadly ovate, sometimes narrowly ovate with coarsely serrate, crisped margins borne on relatively short, thick, dark red-maroon, glaucous petioles (fig. 19). Unlike other subspecies leaf margins do not extend down the petioles as wings, serrations do not terminate in distinct glands, and only rarely are sessile, caducous glands produced in their axils. When leaf blades are broad, they are often broadly rounded-truncate to slightly cordate at the base. Flowers also tend to have oblong-ovate, shortly clawed petals and more glabrate inner sepal surfaces.

The subspecies is often sympatric with the more densely-branched, bushy subsp. *karwinskyi*, which also tends to have red-maroon petioles and thicker, though smaller leaves—characteristics that tend to indicate introgression between the two taxa. It is admittedly sometimes difficult to assign incomplete herbarium specimens with smaller leaves to either taxon, but separation is much easier in the field, for subsp. *latifolia* often produces what appears to be elongate, erect, sucker shoots with their characteristic, very thick, glaucous leaves.

Vauquelinia corymbosa subsp. *latifolia* occurs on limestone slopes in xeric chaparral in northwestern Tamaulipas in the Miquihuana area (fig. 13)

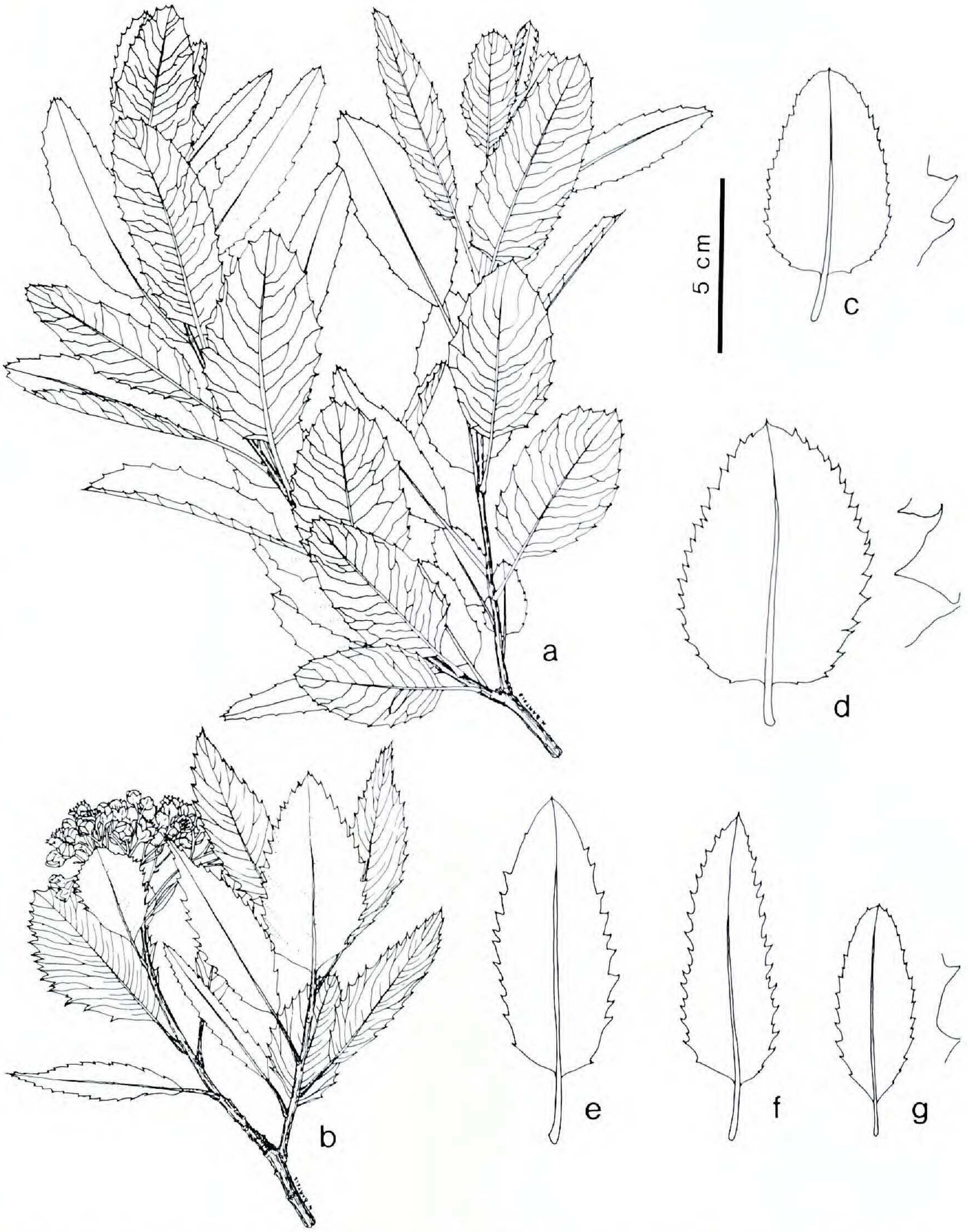


Fig. 19. *Vauquelinia corymbosa* subsp. *latifolia*. All plants from near Miquihuana, Nuevo León. a.-b.—Young stems with characteristic ovate leaves. Note differences in marginal toothing. The characterisitc leaf thickness is not demonstrated in the illustrations. a.—*Henrickson & Hess 19235*. b.—*Hess & Byrne 4713*. c-f.—Leaf outlines showing shape, marginal serrations, and petiole lengths. c.—Leaf from isotype. *Nelson 4481*. d-e.—Variation from a population collection. *Henrickson & Hess 19210*. f-g.—Variation from a population collection. *Henrickson & Hess 19151*. Magnifications as indicated, vertical bar = 1 cm for leaf margin enlargements.

from 1700 to 2400 m in association with *Cercocarpus fothergilloides*, *Rhus virens*, *Agave lecheguilla*, *Hechtia scariosa*, *Berberis gracilis*, *Quercus pringlei*, *Ceanothus greggii*, *Leucophyllum zygophyllum* and species of *Mortonia*, *Litsea*, *Lindleya*, *Gochnatia*, *Dasylirion*, *Dodonaea*, and *Salvia*.

Representative collections: MÉXICO. **Tamaulipas**: Between Hermosa and Miquihuana, 23 Jul 1949, *Stanford, Lauber & Taylor 2684* (NY, US); Cañada de Joya de Gomez, 25 km al NE de al Peña, 26 May 1974, *González-Medrano et al. 7131* (MEXU); 8 km N de la Perdida, 15 Apr 1976, *González-Medrano et al. 8643* (MEXU); Llano del Milagro, 8 km al N de Valle Hermosa, 17 Apr 1976, *González-Medrano et al. 8711* (CAS, MEXU, MO); 10 km NW of Miquihuana, along lower road to Marcela, 23°37′N, 99°52′W, 9 Oct 1982, *Henrickson & Hess 19235* (MOR, TEX); ca 14 km NW of Miquihuana, ca 20 km N of La Perdida towards Marcela, 23°40′N, 99°47′W, 9 Oct 1982, *Henrickson & Hess 19210* (MOR, TEX).

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REFERENCES

AXELROD, D.I. 1979. Age and origin of Sonoran Desert vegetation. Occas. Pap. Calif. Acad. Sci. 132:1 – 78.

DILCHER, D.L. 1974. Approaches to the identification of angiosperm leaf remains. Bot. Rev. (Lancaster) 40:1 – 157.

EMORY, W.H. 1848. Notes of a military reconnaissance. Thirteenth Congress, first session. Ex. Doc. Nov. 41. Washington, D.C.

GOLDBLATT, P. 1976. Cytotaxonomic studies in the tribe Quillajeae (Rosaceae). Ann. Missouri Bot. Gard. 63:200 – 206.

HUMBOLDT, A. and A. BONPLAND. 1807. Plantae Aequinoctiales. Vol 1(6). Latetiae Parisiorum, Paris.

MACGINITIE, H.D. 1953. Fossil plants of the Florissant beds, Colorado. Publ. Carnegie Inst. Wash. Paleontology. 599. Washington, D.C.

_____. 1969. The Eocene Green River flora on northwestern Colorado and northeastern Utah. Univ. Calif. Pub. Geol. Sci. 83:1 – 140, 31 pl.

MARTINEZ, M. 1979. Catálogo de nombres vulgares y científicos de plants Mexicanas. Fondo de Cultura Económica, México D.F.

MAXIMOWICZ, C.J. 1879. Adnotationes de Spiraeaceis. Trudy Imp. S.-Peterburgsk. Bot. Sada, (Acta Horti Petrop.) 6:105 – 238.

RYDBERG, P.A. 1908. Rosaceae. N. Amer. Fl. 22(3):239 – 292.

STANDLEY, P.C. 1918. Six new species of trees and shrubs from México. Proc. Biol. Soc. Wash. 31:131 – 134.

_____. 1922. Rosaceae *in* Trees and shrubs of México. Cont. U.S. Natl. Herb. 23(2):321 – 334.

STERLING, C. 1964. Comparative morphology of the carpel in the Rosaceae. III. Pomoideae: *Crataegus*, *Hesperomeles*, *Mespilus*, *Osteomeles*. Amer. J. Bot. 51:705 – 712. 1964.

_____. 1966. Comparative morphology of the carpel in the Rosaceae. VIII. Spiraeoideae: Holodisceae, Neillieae, Spiraeeae, Ulmarieae. Amer. J. Bot. 53:521-530.

WELLS, P.V., and R.R. JOHNSON. 1964. *Vauquelinia pauciflora* (Rosaceae) from Guadalupe Canyon, Arizona: a species of trees newly reported for the United States. Southw. Naturalist 9:151 – 154.

VOSS. E. G. et al. 1983. International Code of Botanical Nomenclature adapted by the Thirteenth International Botanical Congress, Sidney, Australia, August 1981, Utrecht. etc. XV + 472 pp. (Regnum Veg. 111).

WILLIAMS, K.B. 1971. Ecological and morphological variations of *Vauquelinia californica* (Torr.) Sarg. populations in Arizona. Ph.D. dissertation, Univ. Arizona, Tucson.